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BY

A. G. TANSLEY

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WITH FORTY ONE PLATES, AND NUMEROUS
FIGURES IN THE TEXT

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CONTENTS

ORIGINAL PAPERS

PAGE

Armstrong, J. I., Ingold, C. T. and **Vear, K. C.** Vegetation Map of the Mourne Mountains, Co. Down, Ireland. (With three Maps in the Text) 439

Bates, G. H. The Relation of Leaf Size to Root Structure in *Trifolium repens* (With Plates XXIII and XXIV) 271

Boycott, A. E. The Habitats of Land Mollusca in Britain. (With one Figure in the Text) 1

Buxton, L. H. Dudley. The Willows of the Western Part of the Isle of Wight 304

Chippindale, H. G. and **Milton, W. E. J.** On the Viable Seeds present in the Soil beneath Pastures 508

Clements, Frederic E. The Relict Method in Dynamic Ecology. (With Plates I–V) 39

Davis, T. A. W. and **Richards, P. W.** The Vegetation of Moraballi Creek, British Guiana: an Ecological Study of a limited Area of Tropical Rain Forest. Part II. (With Plates XII–XIV and two Figures in the Text) . 106

De Silva, B. L. T. The Distribution of "Calcicole" and "Calcifuge" Species in Relation to the Content of the Soil in Calcium Carbonate and Exchangeable Calcium, and to Soil Reaction. (With six Figures in the Text) 532

Fenton, E. Wyllie. Grassland Retrogression in Devonshire Permanent Pastures. (With two Diagrams in the Text) 279

Good, R. D'O. and **Waugh, W. L.** The Vegetation of Redcliff Sand: A Contribution to the Ecology of the Humber. (With Plates XL and XLI and five Figures in the Text) 420

Ingold, C. T. *See* **Armstrong.**

Isaac, W. E. The Rate of Decay in Relation to Soil Types and Vegetative Covering in Glamorgan 289

Joshi, A. C. A Supplementary Note on "A Suggested Explanation of the Prevalence of Vivipary on the Sea-shore" 306

Koslowska, Aniela. The Influence of Plants on the Concentration of Hydrogen Ions in the Medium. (With fifty Figures in the Text) . . 396

Martyn, E. B. A Note on the Foreshore Vegetation in the Neighbourhood of Georgetown, British Guiana, with Especial Reference to *Spartina Brasiliensis*. (With Plates XXV and XXVI and one Diagram in the Text) 292

Michelmore, A. P. G. Botany of the Cambridge Expedition to Edge Island, S.E. Spitsbergen, in 1927. Part II. The Vegetation. (With Plates XV–XVII and one Figure in the Text) 156

Milton, W. E. J. *See* **Chippindale.**

Phillips, John. Succession, Development, the Climax, and the Complex Organism: An Analysis of Concepts. Part I 554

Polunin, Nicholas. The Vegetation of Akpatok Island. Part I. (With Plates XXVII–XXXIX and three Figures in the Text) 337

Rayner, M. C. The Mycorrhiza of Conifers: A Review 308

PAGE

Richards, P. W. *See* **Davis.**

Robins, Charles Robinson. Northern Rhodesia; An Experiment in the Classification of land with the Use of Aerial Photographs. (With Plates VI–XI, two Maps in the Text and one Folding Map) 88

Scott, J. D. Ecology of Certain Plant Communities of the Central Province, Tanganyika Territory. (With Plates XVIII–XXII and nine Figures in the Text) 177

Stamp, L. Dudley. Vegetation Formulae 299

Vear, K. C. *See* **Armstrong.**

Watt, A. S. The Vegetation of the Chiltern Hills, with Special Reference to the Beechwoods and their Seral Relationships. Part I. (With two Figures in the Text) 230
Part II. (With one Figure in the Text) 445

Waugh, W. L. *See* **Good.**

Wood, J. G. The Physiology of Xerophytism in Australian Plants. The Stomatal Frequencies, Transpiration and Osmotic Pressures of Sclerophyll and Tomentose-succulent Leaved Plants 69

LETTER TO THE EDITOR—Vegetation Succession and Regional Surveys, with Special Reference to Tropical Africa (Michelmore) 313

REVIEWS 318, 572

BRITISH EMPIRE VEGETATION COMMITTEE 320

BRITISH ECOLOGICAL SOCIETY

Summer Meeting at East Dean, Sussex 321
Fungus Foray at Oxshott 322
Meeting at Cambridge—Annual Meeting 322
List of Members 329

NOTE: Wood Ant Enquiry 577

JOURNAL OF ECOLOGY

ERRATA

VOL. XXI, NO. 1

p. 211, last paragraph, first line: *after* "only" *add* "a tentative one,"

VOL. XXI, NO. 2

p. 321, line 28: *for* "f. and var. *orthothecioides*" *substitute* "f. ad var. *orthothecioides*"

p. 325, line 27: *for* "*Rhacomitrium Lypnoides*" *substitute* "*Rhacomitrium hypnoides*"

p. 328, 4th line from bottom of page: *for* "foehm" *substitute* "foehn"

VOLUME XXII FEBRUARY, 1934 No. 1

THE HABITATS OF LAND MOLLUSCA IN BRITAIN[1]

BY A. E. BOYCOTT.

(*With one Figure in the Text.*)

CONTENTS.

		PAGE
I.	General considerations	2
II.	Species living in wet places	13
III.	Species living in dry places	14
IV.	Human influence	18
V.	"Woodland" species	25
VI.	Calcifuge and calcicole	29
VII.	General summary	34
	References	34

THERE are about 102 species of land Mollusca in Britain, 19 slugs and 83 snails. In this paper I sketch what I know and surmise about their relationships to the habitats in which they are found. Working conchologists know that different species are found in different kinds of places and that the connection is such that experience enables them to predict from the appearance of a place what they are likely to find in it. Comparatively few attempts have, however, been made to systematise this knowledge, and what I put forward here is no more than a framework in which others may perhaps find it convenient to arrange the results of more adequate experience. My own has been mostly in the Midlands and south of England, and this has no doubt coloured my general conclusions: things might appear rather differently to Scotch or Irish naturalists, and it is only by a collation of data from all parts of the country that we can expect to attain our object, which is, I take it, to define and classify habitats from the point of view of the Mollusca themselves and to discover the criteria which render each of them acceptable or repulsive to particular species.

Kendall, Dean and Rankin (**1**) were the first to attempt a systematic oecological account of the Mollusca of an English district (north Lancashire), and Dean (**2**) has pursued the subject for Glamorgan and Kendall (**3**) for Northampton. Swanton (**4**) gives a good description of the Mollusca of different habitats in Somerset. I (**5**) have dealt with a parish in Hertfordshire, Booth (**9**) with the north of Scotland and Alkins (**96**) with north Staffordshire. The *Journal of Conchology* and to a less extent the *Proceedings of the Malacological Society* contain many relevant data especially in recent years: as examples of what may be done for single species, see the accounts of *Vertigo alpestris* by Dean and Kendall (**6**) and of *V. lilljeborgi* by Kevan and Waterston (**7**), and for small areas Quick's (**8**) description of Oxwich sand-dunes and Ellis (**133**) on Market Harborough. In Ireland the oecological outlook has been more prevalent and a wealth of observation and discussion of distribution habits and habitats will be found in Scharff (**11**) on the slugs, Stelfox (**12**) on the land and fresh-water Mollusca of Ireland, of Clare Island (**13**), of the Dingle district (**14**), in an unpublished manuscript on the Mollusca of Ulster which Welch and Stelfox have kindly allowed me to see, and in many papers by these naturalists, Phillips, Grierson and others in the *Irish Naturalist* and the *Irish Naturalist's Journal*. I have not attempted any serious comparison with the Continent: Germain (**77**) gives a summary for France, Geyer (**87**) for Germany and Favre (**89**) a very interesting account for Geneva. For the history of our Mollusca the papers of Kennard and Woodward (**10**) and Kennard (**15**) must be consulted. Their geographical distribution in Britain is given fully by Roebuck (**16**) and for other countries by Taylor (**46**) and Ellis (**150**); Roebuck's census is kept up to date by the Conchological Society.

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[1] This paper is an elaboration of part of the Presidential Address to the British Ecological Society, entitled "Mollusca and Man in Britain," delivered on January 7th, 1933.

I have used a nomenclature which will, I hope, be intelligible[1], and Victorian genera in preference to the fashionable subdivisions which are of more use in the study than in the field. It is hardly possible to acknowledge individually the great help I have had from many friends and correspondents, but my debts to Mr Charles Oldham and Prof. E. J. Salisbury are too large to leave unmentioned.

I. GENERAL CONSIDERATIONS.

(1) The normal *food* consists of the decayed remains of the higher plants, fungi, lichens and algae. The dead leaves are certainly eaten as such even by the smallest species, for recognisable vessels, etc., may be found in their intestines: it may well be, however, that they are taken in as much for the epiphytic algae and moulds as for their own sake. The partly digested vegetables of rabbit and sheep dung are much appreciated. Well-grown wild green plants are very seldom eaten, at any rate in any quantity: as Stahl (**17**) pointed out, they are usually protected either by hairs, oxalate crystals and the like or by juices which are, as he shows, offensive to snails. The only wild plant which I have often seen freely eaten is the burdock (*Arctium lappa*): in woods it is frequently reduced to a skeleton by slugs, and a plant of it which grows in our garden is a favourite food with *Helix pomatia* as well as the common slugs. Wild seedlings are perhaps taken more freely, and A. S. Watt tells me that he has seen beech seedlings destroyed by slugs on a large scale. Flowers also may suffer: Mason (**18**) notes *Arion ater* eating the flowers of *Arum maculatum* and Roebuck (**180**) *Helix striolata* at dandelion, and I have seen *Arion ater* at those of *Scabiosa arvensis*, *Heracleum sphondylium* and, with *Agriolimax agrestis*, at *Caltha palustris*. Cultivated plants such as lettuces and young cabbages and the cotyledons of kidney beans are not protected in the same way, and, in the absence of decayed leaves and rubbish which good cultivation prescribes, the slugs which are adapted to garden life (below, p. 20) eat them

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[1] The following specific names differ from those used by **Ellis** (**150**): the only practical thing to do is to recognise that some species have more than one name.

This paper	Ellis	This paper	Ellis
Limax arborum	marginatus	Azeca tridens	goodalli
Arion minimus	intermedius	Pupa marginata	muscorum
Hyalinia rogersi	helvetica	P. umbilicata	cylindracea
Helix revelata	subvirescens	Clausilia cravenensis	dubia
H. fusca	subrufescens		

Note also: Helix striolata = rufescens, Pupa anglica = ringens.

freely, though I doubt whether most ordinary slugs and snails are particularly fond of them: weeds may protect crop plants (**172**) and wild plants in cultivation may be badly eaten (Marsden-Jones and Turrill (**173**)).

Finding snails walking about on a tree or shrub is no evidence that they are eating it as has been often assumed: their attachment to certain plants (e.g. *Pupa secale* to *Dactylis glomerata* or *Helix nemoralis* to clumps of *Iris foetidissima*) is due to the physical shelter provided by the converging stalks rather than to the food. Experiments in captivity such as those of Gain (**19**) show what molluscs will eat but not what they do eat. Kew's (**22**) scholarly papers contain much curious information.

Cheetham (**20**) says that mosses and liverworts are seldom eaten, but many Mollusca are certainly fond of algae and lichens[1] and make characteristic feeding tracks in scraping them off hard surfaces (tree trunks, rocks, dirty garden glass). These seem to be the natural food of several species, e.g. *Limax arborum* (below, p. 27), the interesting Lusitanian slug *Geomalacus maculosus* which lives on rocks in Kerry, Brittany and Portugal, and *Helix rupestris* (below, p. 15). Most of the abundant slugs and snails that live in dense beech woods with little or no ground floor are also much given to crawling up the tree trunks, presumably to get the Protococcus which in fact they do. Fungi are also favoured by some slugs (**186**), and in autumn most of the toadstools in some woods are more or less eaten by *Arion ater*, *A. subfuscus*, *A. minimus*, *Limax cinereoniger*, *L. tenellus*, etc. The smaller fungi growing on fallen branches are eaten by such snails as *Clausilia laminata*, and Beeston (**27**) says that *Helix obvoluta* is specially fond of Myxomycetes and does not eat green phanerogams at all. Scharff (**11**) concludes that *Limax maximus*, *L. flavus*, *L. arborum*, *Arion subfuscus* and *A. minimus* all feed naturally on food which does not contain chlorophyll, chiefly on fungi, and Cardot (**23**) failed to rear *Limax cinereoniger*, *L. arborum* or *Arion minimus* on carrots and potatoes which did well for *A. hortensis* and *Agriolimax agrestis*: Gain (**19**) found that *Limax arborum* refused "foliage of all kinds."

Testacella appears to be exclusively carnivorous. Some species of *Hyalinia* (*lucida*, *cellaria*, *rogersi*, *alliaria*, *radiatula*, rarely *nitidula*) and also *Vitrina* may also be actively carnivorous in the sense that they will set upon and eat other live snails: they are, however, also and I think mostly herbivorous as the contents of their intestines show. Under stress of close confinement, slugs (*Limax maximus*, *Geomalacus*) also sometimes eat one another, but there is no reason to think that this is a natural habit.

There is in short no evidence that the abundance of Mollusca is, under any ordinary circumstances, conditioned by the quantity of food available (which is always in excess), nor that the occurrence of any one sort is specifically determined by the presence of some special food. Their apparent fondness for, e.g., beech or *Clematis vitalba* is due to their liking the ground on which these plants usually grow, and their apparent dislike of, e.g., heather, pine and bracken to the unsuitability of their substrata. Almost any decayed vegetable with its microflora will do for most species, and those which have a distinct preference for cryptogams do not seem to be very particular within that category: as Miss Lorrain Smith determined for us, for example, *Geomalacus* eats any lichen it happens to be with (**25**) as other animals do (**26**), and her discovery that *Limax arborum* was feeding on *Lecidea sorediza* on rocks on the Westmorland fells (**24**) does not mean that the slug has any specific relation to that uncommon lichen but simply that the slug and the lichen happened to concur. Similarly the preferences of the mycophagous slugs are not exclusive (Elliott and Buller (**28**)). *Testacella* comes nearer to having a specific food than any other: its normal diet is earthworms and its abundance corresponds with their abundance (below, p. 19), but it also eats other slugs (Burton (**181**)) and snails, centipedes, etc.

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[1] Mainly for the fungus constituent: **Schmid** (**21**).

Human influences also illustrate the wide tastes of Mollusca. Every collector knows their fondness for waste paper, cardboard, etc., due I imagine to the size and possibly the grease of printer's ink: they eat starch paste readily when it is offered to them on glass to get records of their feeding tracks. Animal remains (dead birds, old bones, milk, etc.) are also eaten, and I happen rather frequently to have seen *Arion ater* eating the dead bodies of other *ater* and earthworms which have been crushed on the road: it will indeed attack almost anything out of which nourishment can be had, from apples to the conchologist's fingers (Kew (**22**)). Artificial feeding tells the same tale: A. W. Stelfox and C. Oldham have shown by long experience that Mollusca of very diverse natural habitats (e.g. *Helix nemoralis*, *H. aspersa*, *H. arbustorum*, *H. obvoluta* and *Geomalacus*) will all flourish and breed well through successive generations on a mixture of fine oatmeal and powdered chalk spread on cabbage leaves, and no snail or slug to which I have offered the mixture has had any hesitation in eating it. Their fondness for bran is well known to those who devise slug traps.

Some snails have a specific relation to manganese (**29**), and *Ena montana*, *E. obscura* and *Zonitoides excavatus* characteristically contain large quantities. It is, however, a widely distributed element and its availability does not seem to be a factor of any importance in determining the occurrence of these species or, conversely, of the higher helicids which contain very little. Woodland slugs and snails generally contain most, probably because deciduous trees are a mechanism for collecting manganese and depositing it on the surface of the ground at leaf-fall (Bishop (**30**)).

I conclude therefore that *food has no influence either by its quality or quantity on the recurrence of our land Mollusca*, excepting *Testacella* and such meagre habitats as shifting sand-dunes.

(2) *Life histories*. All are normally annuals with a life of 9–15 months except the larger snails (*Helix pomatia*, *H. aspersa*, *H. nemoralis*, *H. hortensis*, *H. arbustorum*) which live for several years, the largest (*H. pomatia*) apparently the longest. Life spans determined from specimens protected in artificial cultures (e.g. 5–6 years and more for *H. aspersa*: Welch (**31**)) are apt to be mis-

leadingly long, though no doubt there is some natural variation and life may be extended if its normal progress is interrupted by periods of dormancy.

None of our species are parasites or commensals and so directly and specifically dependent on another animal.

They are not very prolific though we have no very accurate knowledge of the number of eggs laid wild: the larger kinds may achieve between 100 and 200 a year, the smaller ones less than 50, viviparous species still fewer. Destruction occurs on the usual proportionate scale and only a small minority survive to breed. In a few instances snails play an obligatory part in the life cycles of other animals. Thus the larva of the glow-worm (*Lampyris noctiluca*) feeds on them (commonly *Helix virgata*, also *Hyalinia*), and it is generally understood that nothing else will do; the larva of the rare southern beetle *Drilus flavescens* also needs molluscs (*Helix nemoralis*, *H. hortensis*, etc.). In Scotland *H. itala* has been shown to be the intermediate host of the sheep fluke, *Dicrocoelium dendriticum* (Cameron (**32**)), and other trematode larvae have been found in *Helix hortensis*, *Hyalinia* and *Pupa umbilicata* (Harper (**33**)), one of which has the hedgehog as definitive host. The bird fluke, *Distomum macrostomum*, needs *Succinea* for its cycle. *Agriolimax agrestis* (and in Europe other slugs and *Helix nemoralis*) is the intermediate host of the fowl tapeworm, *Davainea proglottina* (Brown (**34**)), and other cestode larvae invade *Hyalinia* and *Vitrina* (Harper (**122**)) though the harm they do is problematical. Keilin (**124**) describes *Melinda cognata* parasitic on *Helix virgata* at Cambridge and gives an account of the other Diptera which affect Mollusca.

But other animals could get on quite well without Mollusca, and though they eat them pretty freely it is only as an item in a mixed diet. Thrushes' stones are well known, involving usually *Helix nemoralis* and *H. hortensis*, less commonly *H. aspersa*, *H. cantiana*, *H. arbustorum* (Lawson (**136**), Thompson (**147**)), *H. striolata*, *H. itala* and *H. limbata* (Huggins (**137**)). No other bird seems to have the same habit, but smaller snails of various kinds have often been found in the crops of different birds. Rats, voles, mice, hedgehogs, toads and, it is alleged, even rabbits (**184**) also, at least on occasions, eat Mollusca (but without any suggestion of any specific relationships), though some kinds are protected by their large size and thick shell (adult *H. pomatia*[1]) or a garlic smell and pungent taste (*Hyalinia alliaria*) or in some other way (*Limax maximus*, *Arion ater*[2]). In any case I doubt whether the destruction of half- to full-grown snails by these agencies which we see at work is of very much importance. We seldom see young snails much more abundant than the adults will be later on, and the main loss falls I believe on the eggs and infant young. What is responsible for this we do not yet know, nor indeed whether the destructive agent is usually climatic or biotic. The carnivorous larvae of beetles and flies may do a good deal, and I have watched *Hyalinia lucida* eating a hatching batch of *Helix aspersa* eggs with gusto. The sum of the matter seems to be that while artificial circumstances, like wandering fowls or cultivated pheasants, may determine the complete absence of Mollusca there is no evidence that any particular species is localised by the action of destructive agents (though see below, p. 17).

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[1] E. W. Bowell tells me that he has seen young and adults broken on thrush stones at Oxted, and I have lately watched a thrush hammer a young adult to pieces in our garden, but, as **Harcourt-Bath** (**125**) says, the freedom with which the adults (not the young) walk about in the open in the daytime must surely be something more than inexperienced bravado: *Hyalinia alliaria* and *Arion ater* behave in the same way. The vivid appearance of *ater* in all its colour forms might be sematic.

[2] "Which nearly every kind of bird seems to reject as uneatable" (eaten by thrush (Oldham) and in a brown owl: **Bryan** (**134**)); it is a favourite food of the hedgehog (**Moffat** (**35**)) and is also eaten by badgers (**36**).

(3) *Dispersal.* Mollusca are obviously ill adapted to spread far and quickly by their own proper motions. The possible means of dispersal, with special reference to the British fauna, are fully discussed by Kew (**37**). It seems likely that birds[1] and men are the most effective vehicles, and odd living snails have been found far from their natural homes with a frequency which is rather surprising considering how few conchologists there are. Attempts at artificial colonisation in apparently suitable places fail much more often than they succeed: transport is not necessarily followed by oekesis. It is clear on the one hand that the appropriate mollusc does not colonise a newly made habitat with anything like the certainty with which willow herb will occupy any vacant piece of ground or the moth *Cucullia verbasci* find mullein planted in a garden. *Cyclostoma elegans*, for example, is an obligatory calcicole and needs earth with enough lime in it to make it friable and easy to burrow in. In the south of England it occurs on most patches of chalk or oolite which come to the surface in the presence of enough scrub or ground vegetation to afford the necessary shelter even where, as in Hertfordshire, Herefordshire and Norfolk, such patches are few and far between. But I know of no instance where it has colonised suitable fresh habitats which have been made by clearing away the overlying clay in getting chalk, though some of these are within a few hundred yards of a natural home and some of them probably date from Roman times (**5**): curiously enough its transport, nipped on to the leg of a bumble-bee, has actually been seen, probably twice (Kew (**37**), p. 166; Tomlin (**38**)). Similarly the woodland species living in the old forests on the South Downs and the Cotswolds have not spread into the neighbouring beech plantations which were made so freely from about 1750. On the other hand, some kinds seem to move more easily. The brilliant work of A. S. Kennard (**15**) on our recent fossils shows, e.g., that *Helix virgata*, *H. caperata* and *H. cautiana* were not present in Kent in Roman times though they are now widely distributed there and common. French (**39**) notes the spread of *H. virgata* in Essex, Jackson and Standen (**40**) the extension of *H. caperata*, *H. heripensis* and *H. barbara* on to modern sand-dunes, Ellis (**41**) and Cooper (**132**) of *H. virgata* and *H. caperata* on to reclaimed

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[1] E.g. three *Vitrina pellucida* on a meadow pipit caught at the Butt of Lewis lighthouse (Evans (**169**)).

salt marshes and C. Diver of *H. virgata* and *H. caperata* on to the banks of new roads. *Balea perversa* (below, p. 16) must also have been fairly easily moved between its various impermanent homes, aided perhaps by its exceptionally sticky slime (**42**). The domesticated species can also use effectively the chances provided by human movements, gardening, etc. As Stelfox (**12**), for instance, has shown, *Helix striolata* was in W. Thompson's time (*circa* 1840) unknown in the north of Ireland where it is now common in gardens. Similarly, *H. barbara* has been found sitting on a motor car far from its natural habitat (Rice (**43**)), and Orr (**44**) saw fifty-four *H. rupestris* on a piece of rock in transit from Sligo to Belfast. The age of a habitat may therefore explain the absence of the appropriate Mollusca, and if a new good habitat (e.g. a fallen tree trunk with nettles around or any old piece of wood lying in grass) is quickly prolific, it may generally be assumed that the Mollusca found there were already present in small numbers in the neighbourhood: importation must not be assumed too readily, for changes in habitat may only make obvious what was before imperceptible, and it is extremely difficult to be sure that any species is entirely absent from an area.

(4) *Competition* among themselves is an almost negligible factor and it is difficult to find examples of its operation.

Helix nemoralis is a central European species which reaches its northern limit in Britain about Perth: *H. hortensis*, a close ally, extends to Shetland and so through Iceland to north-east America. They live in very similar habitats and in England often occur together in hedgebanks, etc., but on sandhills and grassy places by the edge of the sea *nemoralis* alone is found, often in profusion. About the Firth of Forth both species are found together on the sand-dunes (A. R. Waterston) and this continues to St Cyrus in Kincardine (Booth (**9**), p. 277), but further north, beyond the range of *nemoralis*, *hortensis* is found alone and abundant and on blown sand in Sutherland and Caithness is accompanied by *H. arbustorum*, unknown in similar situations further south though it often enough lives with *nemoralis* and *hortensis* inland in England (Oldham (**45**)). It seems reasonable to interpret these facts by saying that *hortensis* occupies sandhills when *nemoralis* gives it a chance to do so (Taylor (**46**)), and that competition becomes effective because the habitat in question is austere and limited in its possibilities.

It is possible that *Zonitoides excavatus* (calcifuge woodland, below, p. 29) and *Balea perversa* (trees and walls, below, p. 16) also owe their characteristic habitats to necessity rather than choice: they commonly live alone or with few other species in places which snails and slugs in general do not care about.

If a series of localities are arranged in order of merit according to the number of species which are found in them, we see that the kinds which live in the worst places also live in the best: the progression consists in the addition of fresh species without the elimination of those already on the list. *Arion ater* is probably the most ubiquitous species and often lives by itself on acid inhospitable moors; *Agriolimax agrestis* is almost as universal and *Arion minimus* not much more particular: among testacea *Hyalinia alliaria*, *Hy. fulva*, *Hy. radiatula*, *Hy. crystallina*, *Punctum pygmaeum*, *Helix rotundata*, *Cochlicopa lubrica* or *Vertigo edentula*[1] is most likely to be found if any snails at all are discoverable. All these species are also common in the "best" places, which may show nearly forty species in a small uniform area (e.g. old calcareous beech wood). The same is true for the Mollusca of specialised habitats such as marshes or chalk downs: the species which in some places occurs by itself or with few associates will also be found where the full fauna is present. These facts are not compatible with the idea that competition is an important influence, and, with such exceptions as have been mentioned, I do not think that a snail is ever excluded from a locus suitable for it because other snails are there already or that one species can "expel" another as has been assumed by, e.g., Taylor (**47**) and Jackson (**48**). Hence it seems misleading to describe the most abundant species in a place as "dominant" or to use any of the other terminology of competition.

(5) It follows from these considerations that the occurrence of any ordinary snail or slug is determined by its history, its geographical distribution and the nature of its habitat.

(*a*) Under *history* we have to consider its introduction into and spread through this country and the influence on it of past climatic changes and differences in vegetation: Kennard (**10**, **15**) has for instance adduced good molluscan evidence that the south-east of England must have dried up a good deal (leading to the disappearance of some of the snails), and that some at least of the bare Wiltshire downs were once covered with wood or scrub.

(*b*) *Geographical distribution* depends in the main on climatic factors (**49**), though the arrangement of the geology perhaps confuses a south-eastern climate with calcareous strata. As far as one can judge, however, habitats which are, climate apart, fit for the numerous south-eastern species are found beyond their range to the north and west and places suitable for the few western and north-western forms in the south-east.

(*c*) Of the *nature of the habitat* we can, neglecting special cases, say broadly that the main considerations are shelter and lime.

(i) By *shelter* I mean such conditions as secure damp air and provide nooks and crannies into which Mollusca can retire to escape drought and cold and lay their eggs. It depends mostly on the vegetation and on the topography and texture of the ground. Exposure to wind is objectionable, while exposure to damp is necessary: anything which firms the ground and destroys its surface porosity is harmful (such as trampling by men and animals), while rubbish and open humus are always favourable. Logs of wood on the ground are favourite sites because they provide reservoirs of dampness as well as retreats and acceptable food. Dew (which incidentally contains a good deal of calcium carbonate: Smith (**120**)) is the salvation of Mollusca in dry weather, and its incidence and quantity largely depends on the local topography.

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[1] Which of these is found depends apparently on the nature of the badness and decidedly on geography. In England *Helix rotundata* is probably the most catholic and numerous snail, but in the northern half of Scotland and in parts of Ireland (**Taylor and Roebuck** (**127**)) it is, on the English standard, quite uncommon and shows some indication of being calcicole. In the north of Scotland **Booth** (**9**) found *Vertigo edentula* the most frequent species. Of *Hyalinia alliaria* **Thompson** (**147**) said in 1841 of Ireland "all situations seem alike to it, from the exposed sea shore and mountain side to the umbrageous wood."

Dampness is important because it determines the amount of time a mollusc can spend in feeding and breeding. Snails and slugs walk on a film of thin mucus and use up water in the process which is restored when they eat (**78**) or by drinking (Künkel (**51**)): the loss of water from their skin varies with the humidity of the air, and once they are dehydrated beyond a certain point they are immobilised and presently killed. Hence they walk about either at night when the humidity is high or in wet weather. When it is dry, they retire into the surface of the ground or any other small unventilated space where further water loss is minimised and are often troublesome or impossible to find, which is a serious practical difficulty in field work. The effect of wind in drying the surface and driving Mollusca to cover can be readily appreciated by examining open ground and adjacent woodland in wet stormy weather: the active time of snails living in exposed places is evidently liable to be much curtailed, though I do not know of any evidence that they are killed in any considerable numbers by the severest droughts we experience. Different species vary widely in their resistance to desiccation: we have at one end of the scale the xerophiles (below, p. 14) and at the other most of the species of *Hyalinia* which live in sheltered habitats and may die of drought overnight in a dry box. Slugs have no resistance and dry up helplessly, and eggs are particularly susceptible.

Shelter often depends on things being left alone, and *disturbance* by men or animals may mean exposure and desiccation, e.g. by digging over cultivated land, disarrangement and cutting or browsing of vegetation, etc. Natural vegetation in places which are capable of being damp at all conserves moisture remarkably well at the ground-level, which explains why good cultivation is the best way of keeping down garden slugs.

On the other hand, most land snails and slugs are easily *drowned*. If they fall into water their mucus is so diluted that they cannot crawl out. Heavy rain, apart from the actual impact of the drops, may be quite destructive and they do not usually go out into it.

(ii) Every conchologist knows that he is likely to find more species and more individuals in a calcareous than in a non-calcareous place: we have only one calcifuge species and about twenty calcicoles. Oldham's (**182**) fauna of Cheshire and Adams' (**183**) list for Penistone are good examples of what experienced workers find in districts which are predominantly acid. And increasing experience leads me to attach more and more importance to *lime*. Its significance can be appreciated only by *ad hoc* testing of habitats where snails do and do not occur, for there are influential quantities in many places where the geological map makes no suggestion of their presence, and conversely large areas of "chalk" are overlaid with acid clay and are biologically non-calcareous, and much limestone in the north is covered with acid glacial drift. It was a failure to appreciate these facts that led Jeffreys (**52**) to the whimsical statement that "mineralogical conditions have very little to do with the habitat of any of the Mollusca." A certain amount of calcium is of course present everywhere where animals and plants live, and there is no clear-cut division between "calcareous" and "non-calcareous." As it happens, however, the amount of calcium carbonate in soil (about 0·5 per cent.) which gives a perceptible fizzle with acid in the field seems to mark the level at which earth begins to be "calcareous" from a snail's point of view, and I use the word in this rough quantitative sense pending the accumulation of more accurate analyses. Hence a bottle of 20 per cent. hydrochloric acid (which wrapped in a rag does no harm in the pocket) is an essential part of the collector's equipment and each locus can be directly tested. What are essentially the same facts may be expressed in terms of soil reaction as has been done with reference to snails by Atkins and Lebour (**53**) and MacLagan (**148**): this may be practically determined on the spot with a mixed indicator solution and with this advantage over the acid that a distinction can be made between very acid soils of *p*H 5 or less on which hardly any snails will be found and ordinary non-calcareous ground of *p*H 6 or thereabouts. Anyone with the necessary knowledge can also tell a good deal from the plants which are present.

Different calcareous strata produce effects roughly in proportion to their texture and solubility. Chalk and oolite are most favourable, mountain limestone a good deal less, and very hard stuff such as Coniston limestone may have no perceptible influence (Kendall (**1**), p. 354). Insoluble calcium as in calc-silicates, etc., is insignificant.

What may be called unexpected areas of calcareous ground arise naturally or artificially. Naturally, the old red sandstone of Herefordshire contains many patches of cornstone, marked by old lime-kilns, thickets of *Clematis* and such snails as *Helix aspersa* or *Clausilia laminata*; many of the springs and small streams contain very hard water. Similarly, patches of limestone occur in such unlikely places as among the schists of Inverness-shire, and decomposed igneous rocks may give a foothold to calcicole plants and such snails as *Clausilia rugosa*[1] at an altitude of 1800 ft. above Lake Idwal on Snowdon (C. Oldham) and up to 3000 ft. on Ben Lawers (Laidlaw (**119**)): there are also calcareous areas on Cader Idris (Evans (**151**)). Glacial action may calcify a non-calcareous place, and I have described an instance where unexpected calcareous boulder clay explained the surprisingly rich molluscan fauna of a sea cliff bordering the acid slates of Carnarvonshire (**54**). Blown sea sand is frequently overlooked: usually highly calcareous from the comminuted shells of marine Mollusca and Foraminifera, it often enriches an otherwise inhospitable shore and is at any rate one of the reasons why the immediate neighbourhood of the sea is apt to be much more prolific than the ground half a mile inland[1]: greater moisture in ground and air, less disturbance and more salts in the seepage water may be contributory factors.

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[1] With *Limax arborum, Agriolimax laevis, Arion ater, A. subfuscus, A. minimus, Hyalinia alliaria, Vitrina pellucida, Helix rotundata, H. nemoralis* and *H. arbustorum.*

Artificially, man (like earthworms: Salisbury (**130**)) is continually trying to correct the natural tendency of the land surface to become leached to an acid state both by turning the surface over and by adding lime. The discoveries that lime is a good manure and useful for making mortar and plaster seem to be of great antiquity, and in Britain the influence of man in making calcareous habitats is widespread, for he long since became an adept at identifying the stuff he wanted in whatever form it might appear—chalk, limestone, boulder clay, sea sand (used for manure at Bude in 1602), skeletons of marine animals (Kerry) and the shells of Mollusca themselves. In some places (e.g. from South Wales to the Devon coast near Barnstaple and often over shorter distances) limestone was transported before being burned, and calcicole snails may well have been carried with it (Orr (**44**)). Sherlock (**55**) gives an account of the enormous quantities of chalk which have for these purposes been brought on to the surface, and Praeger (**56**) comments on the influence of mortar in allowing calcicole plants (e.g. *Ceterach officinarum*) to spread into acid districts or natives to find a particularly congenial habitat. Burrell (**57**) records a calcicolous moss on a dry gritstone wall enriched with calcareous road dust, and hard limestones and greensands are not infrequently used for road metal. Lime may therefore be looked for wherever man has been.

The main, though perhaps not the only, reason why snails like calcareous soil is the simple one that they need calcium for their shells: if that is so, it seems better to discuss the matter in terms of calcium carbonate rather than of soil reaction, though what is really needed is a comparative calibration of the two scales in terms of Mollusca. All our English wild slugs, whose shells are rudimentary or quite small, are distributed throughout Britain and, as noticed by Fysher (**58**) and Watson (**138**), none of them seems to have any choice between calcareous and non-calcareous soil except possibly *Arion hortensis*: in acid places the abundance of slugs may be in remarkable contrast to the paucity of Testacea. Most of the snails also which are indifferent to lime (below, p. 33) have small thin shells, while those with large heavy shells show a distinct preference for calcareous habitats. In nature very thin-shelled examples of *Helix aspersa*, *H. nemoralis* and *H. arbustorum* have been found in acid places, and artificial feeding experiments show that plenty of powdered chalk in the food leads to a great increase in the weight of the shell both in snails and slugs (Oldham (**59**)).

If small snails are collected by the convenient method (used by that great naturalist F. Buchanan White (**60**)) of taking home bagfuls of dead leaves and surface humus, drying and sieving, it will be found that rubbish from a calcareous beech or ash wood will yield not only more Mollusca but more small life of all kinds than similar material from an acid oak or birch wood or from a beech grove on acid soil. Beetles, bugs, mites, larvae, false scorpions, worms are all affected in the same sense as the snails, which makes one doubt whether the greater facilities for shell making are the only consideration for the snails. Other possible factors are the greater prevalence of earthworms and the consequent better humus and shelter, a larger supply of cryptogams for food and a greater bacterial decomposition of plant remains.

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[1] Tye (**145**) remarked as long ago as 1875 that the superiority of limestone disappears "near the sea, where mollusks appear to exist upon any kind of soil."

These two general factors, shelter and lime, are in experience complementary to one another, and they interact with climate. Acid exposed ground, wet or dry, is the most barren, and considerable parts of the moors which come under this category are, I believe, entirely destitute of snails: sheltered calcareous ground is the most prolific, both in species and individuals. But Mollusca may be unable to occupy exposed calcareous ground, such as the sugar limestone which tops the hills in Teesdale, and acidity may be to some extent balanced by shelter, so that an old damp acid wood may have quite a respectable fauna. Each factor becomes more important if other circumstances are adverse, just as in plants the calcicole habit may be brought out by competition (Salisbury (**131**)).

(6) Since slugs and snails do not form associations or societies of a biological kind with one another or with other animals and plants, the study of the places in which they live resolves itself into an attempt to define the environmental conditions which are specifically acceptable, repugnant and tolerable. Each species has a range of circumstances within which it can live, and this range is plainly wider with some species than with others. Our primary aim should be, I think, to discover the point, presumably somewhere about the middle of the range, which the species finds most congenial and where it flourishes most abundantly. If we are trying to find the main rule, apparent exceptions are for the time relatively unimportant, and too much stress should not be laid on them. They help us to define the tolerated range, which is practically a difficult business because many species are hard to find when, towards the ends of their range, they are present only in small numbers. We shall learn more about this when acquisitive collectors are content to spend more time on unproductive ground.

A few species seem to be abundant wherever they occur, e.g. *Helix virgata* and *H. itala*, common calcicoles, or *Clausilia biplicata*, now known from only three places in England (**61**): their range is presumably small. The majority are abundant in some habitats, infrequent or sparse in others. A few are peculiar in having a wide range without being abundant anywhere: *Hyalinia radiatula*, for example, lives in wet meadows, woods of most kinds, bare chalk downs and generally in grassy places, but it is never abundant or even common. And conchologists will recall other widely distributed species (e.g. *Helix aculeata*) of which they would find it difficult to procure fifty specimens on demand, while of others (e.g. *Helix nemoralis*, *Clausilia rugosa*, *Carychium minimum*) they would know where to go with a good prospect of getting 1000. In this distinction between maintenance and prosperity lies an obscure problem which needs attention. It is perhaps connected with the fact that under conditions where a mollusc can only just maintain itself the few surviving individuals are usually well grown and without any obvious signs of depauperation.

II. Species living in wet places: hygrophiles.

Twelve species are obligatory hygrophiles, i.e. they live in marshes and in the marshy ground by rivers, canals, ditches and lakes and in wet meadows: some of them also in the slacks behind sand-dunes which are at some seasons quite dry. The common species are marked *:

*Agriolimax laevis
*Zonitoides nitidus
Pupa anglica
*Vertigo antivertigo
V. moulinsiana
V. lilljeborgi
Vertigo angustior
*Succinea putris
S. elegans
*S. pfeifferi
S. oblonga
S. arenaria

to which we might add **Limnaea truncatula* which, though nominally a water snail, spends more time out of water than in it. Of these, *Agriolimax laevis*, *Zonitoides nitidus*, *Vertigo antivertigo* and *Succinea pfeifferi* live in wetter places than the others and the last is not far from being amphibious. *S. putris* often occurs with it, but it affects rather drier places and lives in the lush herbage near water rather than among the water plants. *S. oblonga* prefers the mud at the side of ditches and covers itself with it: *S. arenaria* (Quick (**74**)) lives in the slacks at Braunton Burrows with *S. pfeifferi*, *Vertigo moulinsiana* and *Limnaea truncatula*. *Vertigo lilljeborgi* occurs among *Juncus*, etc., on the margins of lakes, often in very acid peaty loci (Kevan and Waterston (**7**)). *Pupa anglica* a relatively uncommon north-western species, lives mostly by trickles of water either in woods or in the open, often without any other hygrophiles. *Agriolimax laevis* is also to some extent a woodland species: of Ireland, Stelfox (**12**) says "moist woods," and in England it is not infrequent in alder thickets and swampy places in woods which are permanently wet. But it is occasionally found in quite dry woods (Oldham (**71**)) in Hertfordshire and Essex, and I have seen it in a dry place by a ruined house 800 ft. up on the Mendips and in a dry ash wood on oolite in Devon. It is not anthropophobe, for it has been found in greenhouses (**11**, **12**).

Excepting *Agriolimax laevis* and *Pupa anglica*, these hygrophiles do not live in shady places: they or their habitats seem to need exposure to the sun and *Succinea* differs from most snails in being positively phototropic. Nor, again excepting *Agriolimax laevis*, are they found round cattle ponds—restricted habitats of a more or less artificial kind and of no great age which they may be deemed not to have been able to reach. None of them shows any preference for calcareous habitats[1], though I am not clear that *Succinea elegans* or *S. arenaria* have been found in acid places.

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[1] The Derwentwater record for *Vertigo moulinsiana* is a mistake (**Kevan** (**73**)), but it occurs in Ireland "on granite" (**Phillips** in (**12**), p. 100).

How these species get through the winter when their homes are often under water is something of a problem. *Vertigo moulinsiana*, as Phillips (**72**) discovered, climbs (along with *Succinea putris*) into the neighbouring bushes and tall herbage: in Hertfordshire it sticks itself high up on to the dead flags, *Glyceria*, etc., and so exposed passes safely through the most severe frosts: experimentally it will survive immersion in water in winter for at least six weeks, and other hygrophile species could likely do the same. Hadden (**143**) also notes *Succinea elegans* hibernating up willow trees, and Kendall, Dean and Rankin ((**1**), p. 357) stuck on rushes.

Twelve other species also frequently occur in damp meadows and marshy places, though they live equally well or better in other habitats: they may often be found abundantly in the rejectamenta of floods:

Agriolimax agrestis
Hyalinia crystallina
Hy. radiatula
Hy. fulva
Punctum pygmaeum
Helix granulata
Helix hispida
H. arbustorum
Vallonia excentrica
Cochlicopa lubrica
Vertigo pygmaea
Carychium minimum

Helix granulata in the south and east of England appears to be confined to quite wet places and lives right down by the water's edge, frequently in colonies. It nowhere deserts such spots, but in Wiltshire, Devon, Cornwall (Horsley (**75**)), north Lancashire (Kendall (**1**)), round Oban (Standen and Hardy (**76**)), and in Elgin it is often also abundant in dry hedgerows and similar places, living closely with such xerophiles as *Helix barbara* (Carnarvon), *H. pisana* (Dean (**185**)) and *Pupa umbilicata* (C. Oldham, South Wales) on both calcareous and acid ground—a difference presumably due to the damper climate of the west. The other species also occur freely in dry places and all of them[1] might be common in e.g. a beechwood on chalk and in many old hedge banks except *Helix arbustorum*, *Vertigo excentrica* and *V. pygmaea* which prefer more open situations. None of them are definite calcicoles, though *Helix hispida* decidedly and *Vertigo excentrica*, *V. pygmaea* and *Carychium minimum* less markedly prefer calcareous ground: the rest are indifferent.

III. Species living in dry places: xerophiles.

(*a*) We have first a group of eight calcicole species which affect open sunny places free from tall herbage, bushes or trees, i.e. habitats which are the antithesis of woodland. Four of them (*Helix virgata*, *H. itala*, *H. caperata*, *H. heripensis*) are typical inhabitants of short calcareous grass as on the chalk downs: they are common especially in the south and near the sea. *H. neglecta* presumably also belongs here, but it is known only from a hedge bank in Kent. *H. cartusiana* has the same habitat, but its range is restricted to south-east England (e.g. the Downs round Lewes) and some ill-known patches in Suffolk[2]. *H. barbara* is mostly a maritime species though it occurs inland in Ireland, at Amberley in Sussex (Robson (**82**)) and about 50 miles from the sea at Aldbourn in Wiltshire: it lives on the south and west coasts from Sussex to Caithness, but not on the east side and sometimes abounds among the marram grass on shifting dunes. *H. pisana* is a Lusitanian snail found among sand-dunes near Dublin, in South Wales (Tenby, Porthcawl) and formerly in Cornwall (St Ives).

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[1] **Germain** ((**77**) II. 558) and **Favre** (**89**) affirm that the dry form of *Carychium minimum* is a distinct species—*C. tridentatum*—*C. minimum* proper being almost exclusively palustral.

[2] Near Havant, **Beeston** found it living in a marsh (**142**).

All the above species live exposed and unprotected on short grass, *H. itala* perhaps to the most extreme degree (for it seems definitely to prefer the hottest and often the steepest (**144**) part of a hillside), while, as Pearce (**80**) pointed out, *H. heripensis* affects rather longer herbage. They all have relatively thick (**81**) white, whitish or black and white shells which help them to tolerate the intense insolation to which they are often subjected and which they escape by climbing up the stalks of any available plants and so getting away from the overheated ground (Astre (**79**)). *H. pisana* (Cardot (**78**)) has unusually concentrated haemolymph. They make little attempt to burrow into the turf or get into any shelter: this may be perhaps because their relatively large size makes this difficult though *H. nemoralis* and *H. hortensis*, which are a good deal larger, tuck themselves away under *Cnicus acaulis*, etc., when they live on open downs.

(*b*) Five other species are found in similar places: they are small and take such good cover in dry sunny weather that they may be difficult to find:

Helix revelata (subvirescens)
Pupa secale
P. marginata (muscorum)
Vertigo britannica
V. cylindrica

The first and last are indifferent to lime, the others calcicole. *Helix revelata* lives on dry grassy slopes overlooking the sea and mostly facing south from Ilfracombe, round Land's End to Plymouth. It may hide among loose stones with *Sedum acre* and *Rumex acetosella* (Gardiner (**83**); Rimmer (**146**)) or under mats of sea campion, and in my experience it does not come out into the open much except in wet weather. It may be wrong to class it as a xerophile, for near Land's End it lives with such species as *Helix rotundata* and *H. granulata* and the crustacean *Talitrus locusta* (Oldham): some at least of its habitats are, however, very dry. *Pupa secale* and *P. marginata* both abound in short dry calcareous grass, but both are also fond of stones and rubble and *P. marginata* of stone walls: it is also maritime on sandhills, etc., which *P. secale* is not. The two species into which *Vertigo* "*minutissima*" is now dissected are rare, with a scattered distribution from Devon to Perth, and live on dry exposed grassy places often on hills: *Vertigo cylindrica* also on sandhills and maritime grass in Lincolnshire and Yorkshire. They hide among loose stones and under larger stones and come out only when it is wet: in some at any rate of their loci quite a number of other Mollusca may be present which are decidedly not xerophile (*Helix aspersa, H. nemoralis, H. striolata*).

(*c*) *Helix rupestris* is definitely what its name implies—rupestral. It is widely spread in Britain, up to 3050 ft. on Skiddaw ((**1**), p. 318), always on natural rock (including a shingle beach: Quick (**8**)), stone walls or buildings and is frequently very local in limited but abundant colonies. It sits close on the rock in blazing sunshine and must become very hot: it is nearly black though old weathered specimens are grey or even whitish: it is also active in winter (Swanton (**4**)). It much prefers calcareous rocks but it is certainly not confined to them, and I have seen it in Herefordshire and the Lake District in places which were wholly negative to the acid test: in Ireland it has been found on basalt, and on mortared buildings far from any limestone area (Stelfox (**12**)).

(*d*) *Balea perversa* is recognised as living "in crevices of walls, rocks, and trees" (but not inside thick woods), and it is very rarely found on the ground. I have never found it there myself and have been able to collect ten certain and possible instances from the literature and the experience of my friends:

"at the roots of decaying herbage on the rocks of the [Plymouth] Hoe" (Bolton (**152**));
"among decaying leaves on Walton Downs, near Clevedon" (Norman in (**4**), p. 42);
"among decaying wood and dead leaves, or lurking in moss" (Tate (**70**), p. 165);
"at the foot of trees, concealed by grass" (Harting (**155**), p. 64);
"among moss and dead leaves" in Devon (Longstaff (**156**));
under a brick at a ruined house at Studland (C. Oldham);
among dead leaves in a wood at Studley near Oxford (Ellis (**157**));
on a rocky landslide on Arthur's Seat (D. K. Kevan);
on flags with *Succinea putris* in Ireland (Stubbs and Adams (**153**));
"on the ground amongst lichens" (Lowe (**154**)).

On trees it lives only on those which afford suitable crannies into which it may retire either by way of a naturally loose rough bark—mostly elm, apple and willow; also thorns on downs (Harting (**155**), p. 89), old gorse bushes (Tomlin (**159**)), walnut (Hadden (**160**)), juniper (Standen (**161**)), hazel (Annandale (**171**))—or by an adventitious coating of moss or something equivalent. It is quite rare on oak[1] or ash (**158**) or on normal beeches, though it may occur on these last if they are mossy or have loose bark from disease or open forks containing dead leaves. In Herefordshire and Lancashire (Dyson (**168**)) it is general and common in the old apple orchards, and in Somerset Swanton (**4**) says "the characteristic species in the apple orchards," though modern orchards probably contain fewer than those conducted in the old-fashioned way. It sometimes comes as near the ground as fallen trees or logs.

On walls and buildings it seems indifferent to lime and occurs on acid unmortared walls as well as those carefully built of, e.g., oolite. Stelfox (**162**) records it on an old watch-house in Donegal 3 miles from the nearest tree, and Whitwell (Roebuck MS.) in the thatch of a barn in Berkshire. It is obvious that none of these habitats are permanent and that some of them are of recent origin (walls, apple trees, possibly elms). Cliff faces (Stelfox (**13**)) and crannied rocks

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[1] In Glamorgan, F. W. Wotton in Roebuck MS. is the only record I know.

(Wintle (**163**)) are its only natural and durable habitat: it is not frequent in such places, and in large parts of Britain no such places exist. Yet it is a common mollusc (if looked for in the right way) and occurs throughout Britain to the Shetlands and is active in cold weather. It is on the whole larger in Scotland than in England and more often matures its lip which White (**60**) attributes to the damper air giving it more feeding time: from its retreats on walls and trees in the south of England it emerges only when it is very wet.

These peculiar habitats have this in common that they are dry, away from the ground and inhabited by few or no other Mollusca or indeed animals of any kind. Under bark on trees *perversa* has usually no companions except perhaps woodlice (*Porcellio scaber*): it is not often found under larger pieces of looser bark on the same tree where there is an accumulation of brown granular sometimes dampish debris (? faeces of woodlice, etc.) in which live worms, *Iulus* and it may be *Hyalinia alliaria* and *Helix rotundata*. So too on walls, while it is sometimes found in close companionship with *Clausilia rugosa*, *Cl. cravenensis*, *Pupa umbilicata* or *Helix rupestris* or some combination of them. I have been a good deal struck by the frequency with which it is confined to those parts of the walls from which these other species are, for some reason or other, absent. The suggestion therefore is that it likes to live away from the ground (geophobic (**5**)), because there is something on the ground which is destructive and that it prefers to live by itself because it is intolerant of competition. For the present it seems best to classify it by the dryness of its habitats.

(*e*) On bare chalk downs and such places where no shelter or accumulated moisture is to be had, a few other Mollusca are found which, though their normal habitats are quite different, must have a fairly substantial xerophilous capacity (facultative xerophiles): to them might be added the species which favour stone walls (below, p. 24):

Agriolimax agrestis
Vitrina pellucida
Hyalinia cellaria
Hy. radiatula
Helix cantiana
H. hispida
Vallonia pulchella
V. excentrica
V. costata
Pupa umbilicata (cylindracea)
Vertigo pygmaea

All these occur in a variety of habitats, damp and dry, except perhaps *Vallonia costata*, which characteristically though possibly not exclusively affects dry places. Except for the three *Vallonia* and doubtfully *Vertigo pygmaea* they can all live in woods. *Vitrina pellucida*, for all its wet appearance and the large amount of body surface exposed in its open shell, retains water well and lives for a long time in a dry box: this helps it to live on downs and sandhills as well as in most other places where snails are found: it is an arctic species, and Laidlaw (**119**) got it on the top of Ben Lawers (3800 ft.).

Helix cantiana (noted by Roberts (**149**)) and *H. arbustorum* both have the curious habit of sitting out on herbage exposed to the sun, especially when they are young. *H. cantiana* lives mostly in long grass, typically on roadside wastes, rarely on sandhills (Hey (**178**)): *H. arbustorum* often in osier beds and wet places as well as on mountains and northern sandhills.

(*f*) Besides controlling their loss of water, xerophiles have other useful adaptations. *Agriolimax agrestis*, *Vitrina pellucida*, *Helix virgata*, *H. itala*, *H. caperata*, *H. heripensis*, *H. barbara*, *H. cartusiana*, *H. pisana* (W. H. Wintle, C. Oldham) and *H. revelata* are all known to breed in the autumn and through the winter—*H. cartusiana* perhaps as early as August, *H. itala* and *Vitrina pellucida* as late as January: most snails lay their eggs in the early summer or have no definite breeding season. By this device the eggs and young avoid the most extreme conditions, and as xerophiles are commonly resistant to cold and hardly hibernate the young can grow during the cool months. When *Pupa secale*, *P. marginata*, *Helix rupestris* and *Vertigo* "*minutissima*" breed in Britain I do not know, but *Pupa marginata*, *P. umbilicata*, *Helix rupestris* and *Balea perversa* are four out of our five[1] viviparous species and there is something which wants finding out about the life history of *Pupa secale* to explain why the young are as uncommon as they are.

IV. HUMAN INFLUENCE.

As has been often remarked, the present surface of Britain is so much the product of man and his animals that little or no "natural land" remains. Since the requirements of domestic plants and Mollusca (shelter, moisture and lime) are much the same, most of the land which has not been cultivated is unsuitable for snails: some ancient woods and sea cliffs are indeed about the only places fit for many Mollusca which have not been seriously altered, for bleak hills and moors are so barren of Mollusca that they hardly come into the discussion. We can therefore ascertain what the snail fauna used to be only from the recent fossils, a branch of study which A. S. Kennard has made his own and which is throwing much light on the past history of both the Mollusca and the land. Broadly speaking man's interest in agriculture has made the land drier and more calcareous, and his sheep and rabbits have prevented the development of open country into scrub and woodland. On the whole, shelter has been diminished and localised and considerable areas have been disturbed and trampled: in the result arable and well-used grassland is mostly nearly free from slugs and snails. His interest in comfort and commerce has destroyed large tracts of old woodland for fuel, and since these were exhausted he has smeared the land with the products of burned coal which are wholly deleterious either by their acidity or from the poisonous tar acids and other substances which smoke and soot contain or, indirectly, by killing the cryptogamic vegetation. Some species (e.g. the larger helices) are more susceptible than others, but a begrimed countryside such as is found near Manchester has a miserable fauna of land Mollusca (Davies (**164**)) which contrasts strongly with the abundance of water snails in the ponds and canals where the soot is diluted beyond its poisonous limits. A certain number of species have found the new habitats which man has made favourable, and to a few they are now essential: the majority dislike them. In sum, man's influence has probably increased the snail population of Britain because for a limited number of species it has provided exceptionally good conditions and the areas which it has desnailed were probably not very prolific before man came on the scene. His activities may have added a few species to our fauna: there is no evidence that they have destroyed any.

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[1] The other one is *Clausilia biplicata*, a geophilous species without any definite association with dryness or wetness (**61**). As vagaries, both *Pupa umbilicata* (**Kevan** and **Waterston** (**7**), p. 307) and *P. marginata* (**Quick** (**8**), **Laidlaw** (**139**)) have been found in marshes.

(i) *Mollusca of houses and gardens: anthropophiles; oikogetons.*

(*a*) *Limax flavus* is domesticated to about the same degree as the house mouse or cricket, i.e. it lives inside houses, in yards, walls near houses, sheds, greenhouses and gardens: it is fond of the grease in the kitchen sink and of garbage in general, and at night may crawl all about the scullery. It has been recorded as far north as Caithness, but it is not common north of the border and as may be imagined is found more in old houses than in new settlements. I know of no record of its occurrence in England away from houses: in Ireland, however, Stanton (Roebuck (**84**)) found one in the stump of an oak tree in a wild wood in Cork, and Phillips (**85**) in a wood in Galway; Stelfox (**12**) says "in some of the old native woods," and Scharff (**11**) "by no means scarce in the country" in woods. In Denmark (Steenberg (**86**)) and Germany (Geyer (**87**)) it is wholly domestic and mostly so in Switzerland (Mermod (**88**), Favre (**89**)), but in France (Germain (**77**)) it is a common wild slug. Its domesticity in England is therefore probably climatic[1].

(*b*) The three *Testacella* slugs (*haliotidea, scutulum, maugei*) are southern or south-western (especially *maugei*), and the only exceptions I know to their being restricted to gardens are the finding of *T. maugei* in an old pasture in Somerset by Hadden (**90**) and "under leaves in a little wood" in Glamorgan (Barrett in Dean (**128**)). Their normal diet is earthworms, and these are known to be much more abundant in gardens than in wilder land. In gardens they seem to be more abundant where heavy manuring has encouraged the worms, e.g. on the site of a celery trench. Worms, therefore, likely enough determine their characteristic habitat. They have no known geological history in this country and may be recent arrivals. In Europe they are also garden slugs but not apparently so exclusively as in this country.

(*c*) *Milax sowerbii* is also a garden slug and sometimes very destructive, feeding underground on roots and tubers (Scharff (**11**), p. 533): its habits have been described by Miles, Wood and Thomas (**92**). Occasionally in the south-west it seems to be wild. Near Salcombe Regis in Devon I have seen it in a natural ash wood a mile[2] from the nearest house and also on the undercliff near the sea, and C. Oldham has collected it in quite a wild oak-hazel wood at Salcombe:

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[1] The house cricket can live "wild" in England and Scotland in hot summers.

[2] Except on uplying wastes, few spots in England are further than this from a human settlement of some kind, past or present. In the south and midlands it is difficult to find any place more than 12 miles from a Roman road (**Close** (**165**) p. 124).

R. A. Phillips found it on some golf links remote from houses in Galway. In France, Germain (**77**) describes it as a western coastal species and does not mention any domestic association: in England it extends as far as Aberdeen, but it is not common beyond Yorkshire. *Milax gracilis*, only lately identified (Phillips and Watson (**91**)), has so far been recorded only from gardens or their immediate neighbourhood.

(*d*) We come next to two slugs, *Agriolimax agrestis* and *Arion hortensis*, in which most gardeners take an unfeeling interest. They find in gardens conditions which are particularly congenial and at the same time occur in abundance in a variety of wild habitats throughout Britain. *Agriolimax agrestis* comes as near as any mollusc to occurring anywhere and everywhere. *Arion hortensis* is also widely distributed, but it needs more shelter and shows a tendency to prefer calcareous ground: in Germany (**87**), Denmark (**86**) and in Norway (Økland (**121**)) it is almost exclusively domestic.

To this group we may add (*a*) *Limax maximus* which though seldom present in any great numbers occurs in many gardens (and even in houses in damp cellars or about a pump) as well as in hedges, woods and other more or less wild habitats. As it does not eat green plants it is harmless. (*b*) *Milax gagates* is sometimes common in gardens and has been found in greenhouses; it more naturally lives in wilder grassy places especially in the west and near the sea. (*c*) *Arion subfuscus* is occasionally a conspicuous garden slug, but it is commonly wild and not very particular where it lives.

An interesting contrast is afforded by the big black slug *Arion ater* which is common throughout Britain, as catholic in its tastes as *Agriolimax agrestis* and yet is hardly ever seen in gardens.

(*e*) Only three snails find in gardens conditions which are particularly favourable and all have in consequence been able to extend their range.

The "common" brown garden snail, *Helix aspersa*, lives wild in woods, hedges, scrubby places and among rocks on the chalk oolite and limestone of the south of England, and near the sea and on sea-cliffs and sand-dunes as far north as Haddington. Throughout its range it is frequent in and about gardens and houses, though in non-calcareous districts it is by no means universal: it has a special liking for stone walls and churchyards. In the north of England and in Scotland it is unknown inland except in such humanised habitats in which it extends to Orkney, where it has been known in gardens for many years (Rendall (**93**)). In consequence there are large areas of Britain in which it is absent or rare. Being a southern species, it hibernates for at least four or five months in central England: for this it needs a sheltered dry place such as a chink in a rock or a hole in a tree or stump, and it is specially fond of holes in walls in which it often congregates in large numbers for the winter: on sand-dunes as at Braunton and Berrow it hides in the loose sand. As Kennard (**15**) has shown it is native only in the south-west and has spread through Britain since Roman times: this he reasonably attributes to its tolerance of cultivation and to the provision of suitable hibernacula by human building. On the cliffs at Land's End it is on the move in mild weather throughout the winter: that hibernation is a real difficulty further north is shown by finding not uncommonly that a considerable proportion, young and old, have died by the spring.

Helix striolata (*rufescens*) is in much the same position, but it is hardier and commoner as a wild species. It is generally common or abundant on any highly calcareous ground in England, but it does not occur on sandhills. It lives in woods, hedge banks and grassy places and hardly hibernates. It occurs profusely at Grange-over-sands and on roadside grass on the Cotswolds at more than 800 ft. But in non-calcareous areas it is confined to gardens, rubbish heaps, etc., and has a great liking for *Arabis* and other mat plants. In Scotland it seems to be exclusively synanthropic up to its northern limit in Kincardine. In Ireland, Stelfox (**12**, **94**) judges that it is native only in the south and has spread northwards by means of gardens. Round Quebec it occurs in immense profusion by houses and among rubbish but not on the wild land near by.

Helix hispida, a very closely allied species, has no special association with man. It often lives with *H. striolata* but is less calcicole and will tolerate drier places (downs, sandhills) in which it is generally dwarfed. The marsh form is also a small one, whereas if *H. striolata* occurs in such places it is of normal size.

Hyalinia lucida has no known preference for lime, but it is wild only in Devon and Cornwall (Kennard (**15**), Wright and Adams (**95**)) and possibly in Glamorgan (Dean (**2**)), as it is in Normandy. Elsewhere in Britain it lives along with man in and near gardens and has so reached Shetland.

(*f*) The precise rationale of this garden habit is not clear, but it seems plain that human habitations and their accessories provide conditions which enable some Mollusca to live where the unqualified soil and climate would be too much for them. Postbridge on Dartmoor, to give another example, is an old hamlet in an exposed position at about 1100 ft., surrounded by bleak acid moorland on which few Mollusca could (and as far as I know only *Arion ater* actually does) live: but *Helix aspersa* is not uncommon among the walls and gardens. The two chief factors are presumably lime and shelter. Adequate calcification is a prime necessity of all horticulture and large amounts of lime are put into most buildings. But ploughed fields which are limed freely are by no means the equivalent of gardens for Mollusca: *Agriolimax agrestis* may occasionally be a nuisance (Peacock (**177**)), but as a rule none of the garden species is present. Hence one attaches importance to the shelter and conservation of moisture which all gardens aim at providing in some degree apart from the rockeries, rubbish heaps and waste corners which the slugs and snails are particularly fond of. In fields possible retreats such as hedges are too far off; similarly cabbage butterflies are not a pest in fields as they are in gardens because no appropriate places for pupation are near at hand (Silvester (**97**), Moss (**50**)).

On calcareous ground the xerophiles, *Helix virgata*, *H. caperata*, *H. heripensis* and less commonly *H. itala*, have frequently been found in large numbers and specially well-grown in stubble fields in the autumn when they are mature. *H. cantiana* (A. S. Kennard) and *H. cartusiana* (A. E. Ellis) have also been seen, and *H. virgata* and *H. caperata* can live in intensively cultivated gardens. This habit is perhaps possible because they breed in the autumn and winter: with autumn sowing this gives the vulnerable eggs and young an undisturbed spell of eight or nine months. Obviously it favours dispersal.

(*g*) In England Mollusca have had 2000 years or more in which to develop and take advantage of a domestic life. As far as I can find none of the native Mollusca in Australia, New Zealand, South Africa or America have adapted themselves to similar houses and gardens in the 100 to 300 years which have been available. *Achatina fulica* (Jarrett (**100**)), starting from East Africa, has progressively spread, as a serious pest in gardens and plantations, to Mauritius, India, Ceylon and China, but such snails and slugs as are found in gardens in Australasia and the United States are importations from Europe which seldom spread beyond domestic influence, though Musson (**99**) mentions *Limax maximus* and Longstaff (**98**) *Arion minimus* and *Hyalinia cellaria* in wild bush in Australia and New Zealand respectively.

(*h*) Besides the definitely anthropophile species, a number of others may be found in gardens, inconstantly and usually not abundantly. What they are depends on the origin of the garden and the thoroughness with which it has been gardened: their occurrence is interesting as it shows that they can bear a moderate or considerable degree of disturbance. Lists are given by Ellis and Watson (**101**). Among the most frequent are:

Arion circumscriptus
Hyalinia cellaria
Hy. nitidula
Hy. crystallina
Vitrina pellucida
Helix rotundata
Helix hortensis
H. hispida
Vallonia costata
Cochlicopa lubrica
Pupa umbilicata
Clausilia rugosa.

In an unproductive area, human settlements may indeed give a good foothold to a number of species without any definite domestic associations. Every collector knows that he may get a pretty fair harvest of *Hyalinia*, *Helix hispida*, *H. rotundata*, *Vitrina pellucida*, etc., among the nettles and rubbish of a farmstead in a barren district, and if the place is derelict so much the better, for the snails have the advantage of the lime and shelter without the inconvenient disturbance. A ruined old house isolated on Dartmoor (**102**) produced *Arion ater*, *A. hortensis*, *A. circumscriptus*, *A. minimus*, *Hyalinia cellaria*, *Hy. alliaria*, *Vitrina pellucida*, *Helix rotundata*, *H. nemoralis*, *Cochlicopa lubrica* and *Pupa umbilicata*; the same favourable effect has been noted in the Highlands (Booth (**9**)) and elsewhere (Roebuck and Smith (**166**)), and is really a commonplace experience. Humanisation tends in fact to improve a poor locality as much as it deteriorates a rich one.

(ii) *Mollusca which are intolerant of human influence: anthopophobes.*

The majority of our Mollusca are, however, "wild" in the sense that they do not flourish under any intensive conditions of human occupation. The reason is that man destroys their characteristic habitats, and if he makes new ones which are suitable it takes a longer time than has yet elapsed for them to be occupied. It is easy to see why draining a marsh or cutting down a wood abolishes the appropriate molluscs, and though a water garden or a plantation may ultimately and adequately reproduce the desirable conditions the corresponding snails are slow to reach the place except by continuity with some surviving focus. There may be something more subtle than this in the reluctance of many species to live with man, but I doubt it. Man cannot let his surroundings alone and is continually trampling, disturbing and altering: he keeps fowls and encourages birds and in a multitude of small ways brings a cumulative pressure to bear on slugs and snails which depend a great deal for their prosperity on being left undisturbed.

We owe our appreciation of the two slugs *Limax cinereoniger* and *L. tenellus* to C. Oldham. They occur throughout Britain (*tenellus* not in Ireland) and are never found except in woodlands which have every appearance of being ancient and which are generally large (e.g. Wyre Forest, Haugh Wood, Harting, Rothiemurchus): the soil and the tree are immaterial (oak, beech, hornbeam, birch, pine, scrub). They do not occur in woods which look like or are known to be plantations, and their discovery is probably as good a piece of evidence as can be had that a wood is on a primeval site (Oldham (**140**)). Hence many of their localities are on ground which is too steep or on soil which is too poor to cultivate. Neither is common or always easy to find; they should be looked for especially in the autumn (when they are well grown) on fungi in wet weather or at night. *L. tenellus* has been recorded for 26 of 112 possible comital divisions (Devon and Kent to Elgin), *cinereoniger* for 74 of 152 (Cornwall and Kent to Sutherland). About 1650 Britain was relatively treeless compared with its condition to-day, and it seems reasonable to attribute their absence from the many woods planted in the eighteenth century to their poor capacity for dispersal as well as to some undefined but necessary maturation of the habitat.

Limax maximus, which is closely related to *cinereoniger*, also lives in old woodlands though the two are not often found together[1]. But it is common also on cultivated ground and lives in gardens and even houses: one is tempted to suggest that it is the cultivated form of *cinereoniger*, and in Norway Økland (**129**) classes it as an anthropochore.

Other sylvestial species which give the impression of being particularly wild are *Helix obvoluta* (Beeston (**27**)), *H. fusca* (Alkins (**135**)), *H. lamellata*, *Ena montana* and *Acme lineata*. Among other groups *Pupa anglica* is wild; it affects moist places with running water either in woods or in the trickles on sea-cliffs, than which there are no more primeval spots in the country. *Helix lapicida* forms an instructive contrast: it would generally be classed as a wild and usually as a woodland snail and such it commonly is: what it really needs are chinks to hide in, and where these are provided naturally, as in the Derbyshire limestone or artificially in garden walls, it ceases to be either woodland or wild.

[1] Since I affirmed (**103**) that they were never associated, Oldham, Ellis, Winckworth and my own observations have supplied six instances, five in calcareous beech woods in south England, the other in an oak-holly wood in Kerry. Roebuck (**176**) records another.

Similarly, *H. striolata* is abundant in many indubitably wild places (ancient woods), but is quite prepared to live with man because he happens for his own purposes to provide acceptable conditions.

(iii) *Stone walls* provide a special type of habitat in which some species flourish to an extraordinary abundance, notably

Helix rupestris
Pupa umbilicata
Vertigo alpestris
V. pusilla
Clausilia rugosa
Cl. cravenensis
Balea perversa

and less commonly

Helix lapicida
Vallonia costata
Ena obscura
Pupa marginata

Except for the two *Pupa* and *Vallonia*, which prefer calcareous surroundings, the stone of which the wall is made and whether it is mortared or not are relatively immaterial. *Pupa umbilicata* and the two *Vertigo* particularly like walls with ivy on them, and a certain amount of cryptogamic vegetation and rubbish is always favourable. Hence walls with the top stones on edge and not flat and under or near trees are often good especially for *Vertigo alpestris* and *V. pusilla* (Dean and Kendall (**6**), Boycott (**24**)), though not so much for *Clausilia*. Densely mossy walls and those with much grass, etc., are however unproductive (Petch (**179**)), as are thin loose walls and walls in exposed places. Walls backed with earth are as good for *Clausilia* and *H. lapicida* as those open on both sides, but I am not certain that this holds for the other species.

Vertigo alpestris, an arctic-alpine species with a limited north-western distribution, is in England[1] hardly known apart from walls. *Clausilia cravenensis*, also north-western, much extends its range and frequency by the walls: it lives otherwise only on natural calcareous rock (to 1500 ft. (**174**)) except on the Durham coast where it inhabits damp clayey banks on the sea-cliff (Harrison (**141**)) as *Clausilia rugosa* does in Carnarvon and Cornwall. *Helix rupestris* too has no other habitat except rocks on which (if they are available) it is at least as frequent and abundant: it is the only species in the list which apparently finds no advantage in the walls which it has not got in its natural, very wild homes. The others live in a variety of habitats in which, however, they are never more abundant than on suitable walls, though *Pupa umbilicata* may be as numerous in old quarries and *Ena obscura* in beech woods. As would be expected, several (*Helix rupestris, Pupa umbilicata, P. marginata, Balea perversa*) are viviparous xerophiles (above, p. 18), but the others lay eggs in the ordinary way and have no great liking for dry places. What the element in common is I do not know—perhaps a preference for being away from the ground and avoiding some enemy ((**5**), p. 238). *B. perversa* (above, p. 17) certainly has this habit: *Clausilia rugosa* and *Pupa umbilicata* may live[1] up trees (e.g. old pollard willows or diseased beech trees with much loose bark) and *P. umbilicata* characteristically on the little ledges in quarry faces, but they are often enough on the ground. Earthy walls with so much vegetation that they are not very different from the ground (as in western Cornwall) do not have the favourable quality, whatever it is. Perhaps on the other hand walls provide a version of natural rocks superior to the originals in providing better shelter and of much more general occurrence: *Helix rupestris* despises shelter and gains nothing but a wider range. It may also be significant that though several of these mural species often occur together, one of them is generally much more abundant than the others.

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[1] Not on the Continent: in Denmark (**86**) and Germany (**87**) woodland, in Switzerland (**88**) also in rocky places. *Parietaria officinalis* is a rock species in southern Europe, but in the north is practically confined to walls (**Lee** (**167**)).

Historically the facts are interesting, for all walls are more or less modern and many can be approximately dated. Thus the floor of Langdale in Westmorland was dense forest till iron smelting cleared it in the sixteenth century (Ward (**104**)): it was brought into cultivation and the walls built about 1600 and later (W. G. Collingwood). They now harbour *Vertigo alpestris* and often *V. pusilla* in most suitable places, though neither can now be found on the neighbouring rock or in the screes or woods (**105**). It is possible that such small species are blown about the country on the dead leaves on which they like to sit, as Gulick (**106**) supposes for the pulmonate microfauna of oceanic islands.

Railway embankments, ballast heaps, quarries and other human habitats often provide conditions favourable to some Mollusca, but I do not propose to discuss them in detail.

V. "WOODLAND" SPECIES.

Woods as such have no characteristic fauna. What they show in the way of Mollusca depends in the main on their age, the soil in which they are growing and on the degree of shelter (always fairly well provided) and conservation of moisture. Beech and ash woods are the most productive because and if they are on calcareous ground: oak, birch and fir[2] are relatively sterile because they are usually on acid soil and the two latter on over-dry ground. Beech and ash on acid ground are no more productive than oak on clay, as may be seen by comparing the fauna of the chalky western escarpment of the Chilterns with that of the plateau beech woods on clay behind them or the beeches in Savernake Forest (Hurst (**126**)). Acid oak woods in the west will generally be richer than those in the east because they tend to be damper: similarly woods in valleys are better than those on hills, and the foot of the slope on which most woods lie is likely to be more productive than the upper parts because of the larger supply of calcium and water (Salisbury (**109**)). There is therefore no specific relation between trees and Mollusca. The fauna of many acid woods is very poor both in species and individuals. An old dry oak wood may yield only a few *Helix rotundata* and *Hyalinia alliaria*, perhaps *Hy. crystallina*, *Hy. fulva* and a few slugs: ten species in one wood would be exceptional. Rothiemurchus Forest has a fair slug fauna (*Limax cinereoniger*, *L. tenellus*, *L. arborum*, *Arion ater*, *A. subfuscus*, *A. minimus*) and no snails. On the other hand woods can produce more than any other locus and what they may contain is perhaps best shown by the two following lists—one for Whitcombe Wood by Birdlip in Gloucester, an ancient beech-ash wood on oolite, the other for Torc Woods at Muckross in Kerry, an acid wood predominantly oak and rather wet: each has after its own kind an uncommonly rich fauna. The species in common are marked *:

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[1] *Living* up trees must be distinguished from the common habit (anabatic) of climbing up tree trunks which many geophilous molluscs have.

[2] I doubt whether conifers are *per se* as repulsive to snails as is generally thought. Apart from the poor soil, their plantations are so dense that there is no ground flora. Mollusca do not appear particularly to dislike odd firs planted in, e.g., a calcareous ash wood and will crawl on to and up them in wet weather (cf. **Favre** (**89**), p. 323).

Whitcombe Wood—37.

Limax cinereoniger
L. maximus
L. tenellus
*L. arborum
Agriolimax agrestis
*Arion ater
*A. subfuscus
A. hortensis
*A. circumscriptus
Vitrina pellucida
*Hyalinia cellaria
*Hy. alliaria
*Hy. nitidula
*Hy. pura
*Hy. crystallina
*Hy. fulva
*Punctum pygmaeum
*Helix rotundata
H. hispida
H. striolata
*H. aculeata
H. lapicida
H. arbustorum
H. pomatia
H. aspersa
*H. nemoralis
H. hortensis
Ena montana
E. obscura
Cochlicopa lubrica
Pupa secale
Clausilia laminata
*Cl. rugosa
Cl. rolphii
*Carychium minimum
Cyclostoma elegans
*Acme lineata.

Torc Woods—24.

*Limax arborum
*Arion ater
*A. subfuscus
A. minimus
*A. circumscriptus
*Hyalinia cellaria
*Hy. alliaria
*Hy. nitidula
*Hy. pura
*Hy. crystallina
*Hy. fulva
*Punctum pygmaeum
*Helix rotundata
H. fusca
*H. aculeata
H. lamellata
*H. nemoralis
Pupa anglica
P. umbilicata
Vertigo substriata
V. edentula
*Clausilia rugosa
*Carychium minimum
*Acme lineata

Further search would no doubt add several species to each of the lists. If we analyse them we find that of the seven species found at Torc and not at Whitcombe, *A. minimus*, *V. endentula* and *P. umbilicata* are probably defects of collecting and *Helix lamellata*, *Pupa anglica*, *Vertigo substriata* and *Helix fusca* are north-western and uncommon as far south as Gloucester, and Whitcombe is not wet enough for *Pupa anglica*. Of the twenty found at Whitcombe and not at Torc, geography accounts for *Limax tenellus*, *Helix lapicida*, *H. arbustorum*, *H. pomatia*, *Ena montana*, *Pupa secale*, *Clausilia laminata*, *Cl. rolphii*, *Cyclostoma elegans* and probably for *Helix hortensis* and *Ena obscura* and the soil for *Helix striolata*, *H. hispida*, *H. aspersa* and probably *Arion hortensis*: *Limax cinereoniger* or *L. maximus*, *Arion agrestis*, *Vitrina pellucida* and *Cochlicopa lubrica* are probably defects of collecting. There are seventeen species in common and of these only one (*Acme lineata*) can be reckoned to have any close association with woods though these would be the easiest places in which to find *Limax arborum, Punctum pygmaeum, Helix aculeata* and *Carychium minimum*. *Acme*, too, is not confined to woods but flourishes in damp places on some sea-cliffs with no more than a herbaceous vegetation (Standen (**107**), Welch (**108**), Stelfox (**12**), p. 121). The others are, except *Limax arborum*, common species found in a variety of situations, some almost "anywhere."

Two sylvestral species (*Zonitoides excavatus*, western calcifuge and *Helix obvoluta*, south-eastern calcicole) are not in either list, though the former actually occurs at the bottom of Whitcombe Wood on acid Lias clay (E. P. Blackburn). And there are also three others missing (*Hyalinia radiatula, Azeca tridens* and *Vertigo substriata*) which occur in woods. Adding these five to the forty-four found we have half our British fauna and from them we may select the following thirteen as having special woodland alliances:

Limax cinereoniger
L. tenellus
L. arborum
Zonitoides excavatus
Helix fusca
H. lamellata
H. lapicida
Helix obvoluta
Ena montana
Clausilia laminata
Cl. rolphii
Pupa anglica
Acme lineata

Of these *Limax tenellus* and *L. cinereoniger* are most nearly confined to actual woods. *L. arborum* lives also on cliffs and rocks in heather and grass moors, up to 3100 ft. in Kerry (Stelfox (**14**)) and 2500 ft. on Ben Alder (Carruthers (**170**)) and even in gardens (North and South Wales, Newcastle): its occurrence is determined by the presence of hard surfaces on which its favourite algae and lichens grow, and these may be furnished either by trees or rocks: it never lives in grass. *Ena montana* is mostly found in calcareous beech and ash woods from Suffolk to Somerset, but it occurs in roadside hedges at several places near Bruton and in limestone screes with bushes of thorn and hazel at the west end of the Mendips (picture in Swanton (**4**)). *Helix obvoluta*, the classical snail of the Sussex beech woods, lives also in old hedges and scrub without beech in its area. *Clausilia laminata* and *Cl. rolphii* can prosper in hedges and a variety of scrubby calcareous loci. *Helix fusca, H. lamellata* and *Pupa anglica* as well as *Acme* flourish on some sea-cliffs with little vegetation as described by Stelfox in the Clare Island survey (**13**). *Helix lapicida* (above, p. 23) may abound away from woods, and in a favourable district in Wales *Zonitoides excavatus* is generally distributed under stones and logs, etc., though in Ireland (**127**) it is more definitely associated with old woodlands.

"Woods" is evidently not a significant category for the Mollusca. Old self-planted hedges of mixed trees and bushes obviously go with them, and also scrubs and near-scrubs and undercliffs of various kinds: these represent ancient and relatively undisturbed natural habitats. The verbal difficulty arises when it appears that we should include also the nooks and ravines on bare sea-cliffs. Rather unfortunately the term "woodland" has been applied to this collection of habitats which without any great external similarity evidently have a common element in their relation to Mollusca. With "woodland" there is also an implication of "wild" so that in effect the word has come to mean almost any unsophisticated place other than a marsh, a bare grass down, a heath or a moor, practically excluding modern plantations. The nomenclature is unsatisfactory, but the conception seems to represent the fact that there is a series of habitats which "woodland" species frequent, shelter, moisture and stability being the germane factors.

It is of some help in defining the position to enumerate the species which are not found in woods (* indicates sometimes found):

Anthropophiles: *Testacella* (three species), **Limax flavus, Hyalinia lucida.*

Hygrophiles: **Agriolimax laevis, Zonitoides nitidus, Helix granulata, Vertigo antivertigo, V. moulinsiana, V. lilljeborgi, V. angustior, Succinea* (five species).

Xerophiles: *Helix rupestris, H. virgata,* **H. caperata, H. heripensis, H. itala, H. barbara,* **H. cantiana, H. cartusiana, H. pisana, H. revelata, Pupa marginata, Vertigo britannica, V. cylindrica,* **Balea perversa.*

Incertae sedis: *Milax gagates,* **Hyalinia rogersi, Vallonia* (three species), *Caecilioides acicula* (below, p. 31), *Vertigo pygmaea, V. alpestris,* **V. pusilla. Clausilia biplicata, Cl. cravenensis.*

The anti-woodland species are thus mostly those with special habitats, which corresponds with the general conclusion that "woodland" provides exceptionally well the conditions which many Mollusca find congenial. Most of our common slugs and snails are in fact "woodland" species whose demands are modest and open to some compromise and adaptation and whose capacities or facilities for dispersal and oekesis are perhaps greater than those of the more exclusive species which remain more or less confined to what is woodland in the ordinary sense. Their habitat cannot be precisely defined, for they live "anywhere" where there is shelter and moisture and the various species may be arranged on a scale (**110**) of minimum requirements, beginning with those which are least particular and occur in the worst (acid dry exposed) places such as

Arion ater
A. minimus
Agriolimax agrestis
Hyalinia alliaria
Hyalinia crystallina
Hy. fulva
Helix rotundata
Vertigo edentula[1]

passing through others which are more exacting, as

Arion circumscriptus
Hyalinia nitidula
Hyalinia pura
Carychium minimum

and those which generally need a little lime, as

Hyalinia cellaria
Helix hispida

---

[1] Several times (**118**) recorded on bracken, generally innocent of all Mollusca.

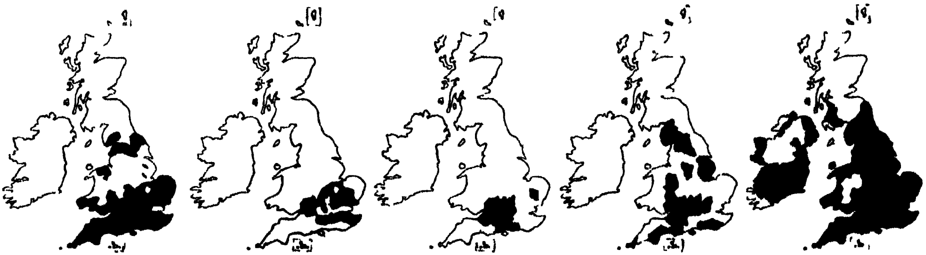
to the definitely calcicole species and those with specialised habitats in wet, dry or domesticated circumstances.

VI. CALCIFUGE AND CALCICOLE.

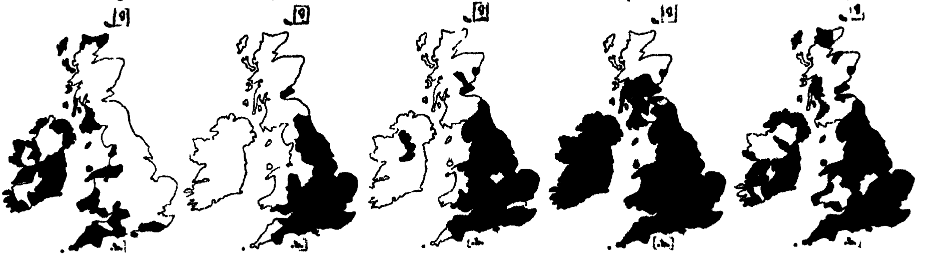
Lime is such an important factor that it will be well to reconsider the fauna in its terms, the classification cutting across the groups which have already been defined.

(*a*) *Zonitoides excavatus* is our only species which is definitely *calcifuge.* It is a woodland species and has never been found living on calcareous soil though it has been discovered in late Pleistocene cave earth in mountain limestone near Carnforth (Jackson (**62**)), in stalagmite from a limestone cave on Caldey Island (Wintle (**63**)), and in calcareous tufa in the Isle of Wight (A. S. Kennard). Shells are washed into these deposits from a variety of habitats, and the *excavatus* may well have come from a leached acid surface in the neighbourhood or been brought from elsewhere by birds (Kennard (**64**)). These occurrences therefore do not invalidate the proposal that it is a precise indicator of silicious soil. Prof. E. J. Salisbury has been good enough to analyse a number of soil samples from *excavatus* loci for me and has found from nil to 0·04 per cent. of carbonate. Its occurrence is also conditioned by its western distribution: in the well-searched south-east it is distinctly rare, and it is absent from East Anglia and the whole of the east of Scotland: in Ireland it fails in the east and in the central limestone plain. It is not often common or abundant and is frequently colonial. It seldom has many molluscan companions, which is the almost necessary consequence of its calcifuge habit and may mean that it is intolerant of competition. In captivity it eats oatmeal and powdered chalk freely without coming to any harm, and in my hands has produced young after living a year in highly calcareous soil along with *Cyclostoma elegans.* This suggests, though it does not prove, that in nature it lives where it can rather than where it would.

(*b*) The clearest obligatory *calcicole* is *Cyclostoma elegans* which is never found except on highly calcareous soil (at least 5 per cent. of carbonate and generally much more). It is a southern species (Cornwall and Kent to North Lancashire) and lives mostly underground, needing a loose friable soil into which it can burrow. It needs a certain amount of shade and shelter: it does not live on open bare downs nor much in dense woods but likes scrub, hedge-banks and bushes, often with loose stones. It often occupies quite small suitable areas isolated in a non-calcareous countryside as at Aldenham (**5**), or on cornstone in Herefordshire or "in great profusion on the bosses of chalk that appear among the overlaying tertiary gravels and clays" in Norfolk (Woodward in (**70**)). French (**39**) says of Essex that it was abundant in Pleistocene and Roman times and is now very local owing to the leaching of the surface, and Jackson (**69**) finds the same in Lancashire. Chalk oolite and limestone seem equally satisfactory: beyond their western range it has been found on marine

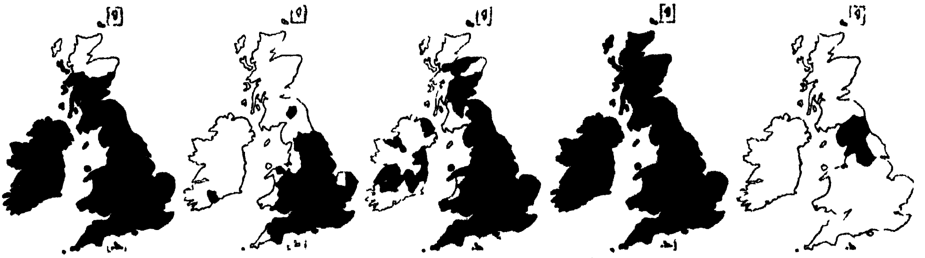


Cyclostoma elegans *Helix pomatia* *Ena montana* *Pupa secale* *Helix virgata*



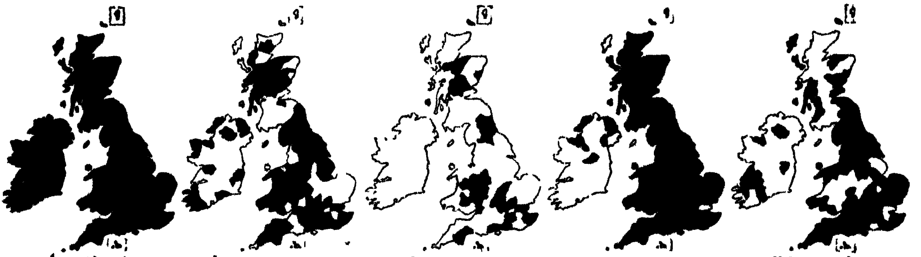
Helix barbara *Helix cantiana* *Clausilia laminata* *Helix striolata* *Pupa marginata*

CALCICOLES

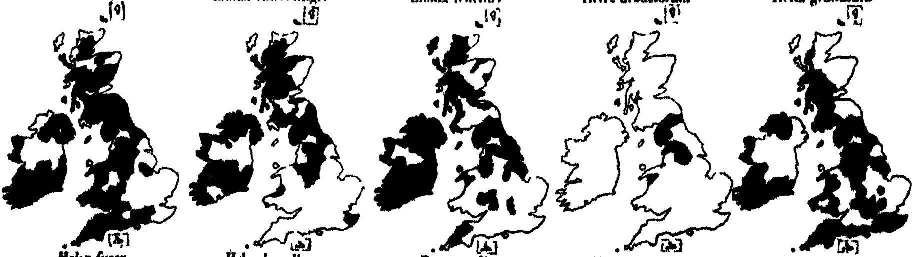


Helix nemoralis *Helix lapicida* *Ena obscura* *Pupa umbilicata* *Clausilia cravenensis*

PREFER LIME



Arion ater, etc *Limax cinereoniger* *Limax tenellus* *Helix arbustorum* *Helix granulata*



Helix fusca *Helix lamellata* *Pupa anglica* *Vertigo alpestris* *Zonitoides excavatus*

INDIFFERENT CALCIFUGE

Fig. 1. Showing distribution of Mollusca in Britain in relation to lime.

sandhills at Woolacombe (Longstaff (**66**)) in Devon, and in Cornwall at Perranporth (J. H. James in Roebuck MS.), near Padstow (A. Gardiner, *ibid.*) and in a prehistoric deposit at Harlyn Bay (Kennard (**67**)). In Wales too H. E. Quick finds it among bracken on sandhills at Llangenneth in Glamorgan, and Montagu (**68**) noted it "close to the sea, at the roots of fern, to the west of Tenby." It is unknown on inland non-calcareous sands, and the chemical composition of its habitat is evidently more important than its physical texture (**65**), though in sand it can apparently do with less calcium than in loam.

(*c*) The following eight also appear to be obligatory calcicoles though they do not all need such highly calcareous soil as *Cyclostoma elegans*:

Helix virgata (p. 14)
H. itala (p. 14)
H. cartusiana (p. 14)
H. obvoluta (p. 27)
Helix pomatia
Ena montana (p. 27)
Caecilioides acicula
Pupa secale (p. 15)

Helix virgata extends to the south of Scotland, *H. itala* by the sea to Caithness; these two with *Caecilioides acicula* occur in Ireland: the other five are southern and *C. acicula* is not known in Scotland. *Helix pomatia* lives scattered in colonies from Kent to the Cotswolds and Northampton in thin woods, coppices, open hedges (the "shaws" of Surrey), quarries, railway cuttings and similar moderately shaded places: also in gardens (in which it is harmless) and it has often been deliberately colonised. *Caecilioides acicula* is subterranean, seen more often dead than alive and found in the talus of oolite quarries (H. G. Thornton) or of limestone cliffs (E. Collier) with a preference for magnesian limestone in Yorkshire (Emmet (**111**)) and Ireland (Grierson (**112**)) and in river rejectamenta: also in gardens (**175**). *Helix neglecta*, *H. fruticum*, *H. elegans* (*terrestris*) and perhaps *H. limbata* are also probably calcicoles, but they occur in so few places (all in the south) that the data are imperfect.

(*d*) The next eleven species are also, I believe, in the same category: they are certainly nearly always in calcareous places and I do not know of their having been found in habitats which, *on being tested*, proved to be non-calcareous. They are all more or less southern or maritime (*Helix caperata*, *H. barbara*, *Pupa marginata*) in distribution.

Helix caperata (p. 14)
H. heripensis (p. 14)
H. barbara (p. 14)
H. cantiana (p. 17)
H. striolata (p. 21)
H. aspersa (p. 20)
Helix pisana (p. 15)
Pupa marginata (p. 15)
Vertigo britannica (p. 15)
Clausilia laminata (p. 27)
Cl. biplicata (p. 12)

About *Clausilia laminata* there is perhaps some doubt: Alkins (**113**) finds it on gritstone walls in north Stafford, but such loci need special examination before they can be passed as non-calcareous.

(*e*) Between this group and the next the division is not at all clear. But I try to make a list of the interesting and indicative species which prefer a calcareous habitat, especially under adverse climatic or topographical conditions, but are also found sometimes, and generally in small numbers, in non-calcareous places: abundance has to be considered as well as occurrence. Presumably the line which separates the places where they live from the places they do not occupy is not identical with our arbitrary distinction between "calcareous" and "non-calcareous": it would be strange if it were. Those marked * have a limited distribution to the north though they all extend into Scotland: *Clausilia cravenensis* occurs only in the north of England:

Hyalinia cellaria
Hy. pura
Helix rupestris (p. 15)
*H. hispida (p. 21)
H. aculeata
*H. lapicida (p. 23)
*H. nemoralis
H. hortensis
Vallonia pulchella
V. excentrica
V. costata
*Ena obscura
*Azeca tridens
Pupa umbilicata
Clausilia cravenensis (p. 24)
Carychium minimum

Hyalinia cellaria, *Helix hispida* and *Carychium minimum* are three useful indicator species which, found in any numbers, without any definite calcicoles, raise a suspicion that the soil will very likely fizzle with acid though it may not: they are decidedly more frequent and abundant on calcareous ground though *Hyalinia cellaria* may be fairly plentiful in moist well-sheltered silicious places. *Pupa umbilicata* is much the same: it may live with *Zonitoides excavatus* but much prefers natural or adventitious lime, its scarcity on the chalk (Swanton (**114**)), Hurst (**126**)) and in the south-east of England being due to climatic dryness while in Hereford it can be found on almost every ivied mortared wall. *Helix lapicida*, *Ena obscura* and *Azeca tridens* are calciphile species which occasionally overlap into acid places. In this country where *Helix lapicida* occurs on natural rock it is always calcicole, but I have seen it in abundance on an old unmortared churchyard wall of non-calcareous stone at Garway in Hereford and on acid walls at Lynton in north Devon: at Porlock it lives (dwarfed) on beach boulders (Hadden (**115**)). *Ena obscura* is one of the most luxuriant species in calcareous woods, but odd specimens turn up in hedges and other places which are at any rate not highly calcareous, and Alkins (**116**) found it in profusion on grit walls in Staffordshire and Grierson (**117**) on a granite wall in Wicklow; at its northern limit in Scotland (Elgin, Inverness) it is known only from patches of limestone. *Azeca tridens* lives in colonies mostly on calcareous ground but also with *Zonitoides excavatus* in the moist sheltered woods of the Marple valley. *Helix nemoralis* and *H. hortensis* are abundant on sandhills and by the seashore, on roadside and railway banks, in colonies on the chalk downs and sometimes in beech and ash woods—always I believe on more or less calcareous soil. But both species occur occasionally in small numbers in acid places where conditions are otherwise favourable, e.g. *nemoralis* on boulder clay in Hertfordshire, among bracken in Carnarvon and Kerry and among heather on Holyhead Mountain (C. Oldham), *hortensis* in birch woods in Inverness and in the Dartmoor valleys. Apparently if there were no calcareous ground these species would still exist but they would be considerable rarities: the same is presumably true of the others in this group. Clench (**123**) has seen

Helix nemoralis rasping away the shells of their dead fellows in an American locus poor in lime as I have seen *H. rotundata* do in a *Zonitoides excavatus* place.

(*f*) The last group consists of forty-five species which are I surmise indifferent to lime in the sense that they may occur freely in both acid and calcareous loci, though as in the preceding group if I wanted a number of specimens of many of them I should look more hopefully in calcareous places:

Limax cinereoniger
L. maximus
L. arborum
L. tenellus
Agriolimax agrestis
A. laevis
Milax gagates
Arion ater
A. subfuscus
A. hortensis
A. circumscriptus
A. minimus
Vitrina pellucida
V. major
Hyalinia lucida
Hy. rogersi
Hy. alliaria
Hy. nitidula
Hy. radiatula
Hy. crystallina
Hy. fulva
Zonitoides nitidus
Punctum pygmaeum
Helix rotundata
H. granulata
H. fusca
H. lamellata
H. arbustorum
Cochlicopa lubrica
Pupa anglica
Vertigo antivertigo
V. substriata
V. moulinsiana
V. pygmaea
V. alpestris
V. pusilla
V. angustior
V. edentula
V. cylindrica
Balea perversa
Clausilia rugosa
Succinea putris
S. pfeifferi
S. oblonga
Acme lineata

Thirteen other species about which the evidence is incomplete ought possibly to come here too.

(1) I am not sure that the three sorts of *Testacella*, *Limax flavus*, *Milax sowerbii* and *M. gracilis*—all domesticated species—are found away from calcareous surroundings: nor do I know of acid stations for *Succinea elegans* or *S. arenaria* (Braunton Burrows only).

(2) Similarly I have no evidence that *Vitrina pyrenaica* (only in Meath and Louth), *Geomalacus maculosus* (west Cork and Kerry), *Helix revelata* (coastal grass from Ilfracombe to Plymouth), *Vertigo lilljeborgi* (acid marshes in Ireland, the Lake District and Scotland) or *V. genesii* (Queen's County) have been found living in calcareous places, but there is no reason to think that they would object to doing so.

In this group shelter and moisture are the chief considerations. *Hyalinia rogersi* is abundant on chalk, often in old chalk pits, in Surrey, Hertfordshire, and Devon, and equally on the acid slates of the Glaslyn valley in Carnarvon. *Arion ater* abounds on bare chalk as well as on Exmoor or the hills in north Wales. *Helix lamellata* is north-western and so usually lives in non-calcareous places but it is abundant on limestone in north Lancashire: two other north-western species (*Pupa anglica* and *Vertigo substriata*) occur on a calcareous cliff at Nevin in Carnarvon: *Helix fusca* on the carboniferous limestone in the Forest of Dean. *Vertigo edentula* may be found in *Sphagnum* or a chalk beech wood, *Helix granulata* on the chalky slopes of Old Sarum and on the slates of west Cornwall, *Vitrina pellucida* with *Zonitoides excavatus* or *Cyclostoma elegans*. Of species with a limited distribution, *Vertigo alpestris* (p. 24) prospers on limestone or acid walls, with or without mortar, and *Vitrina major*, which in England is at the northern limit of its distribution, lives on acid clay at Burnham Beeches close to *Zonitoides excavatus* and in a beech-ash wood on oolite in Gloucester with *Cyclostoma*.

Looking at the list of these indifferent species one is struck by the fact that it contains only one (*Helix arbustorum*) with a substantial shell and none of the other highly developed and good-sized helices which are mainly southern in Britain and of rather limited European range, while there are many slugs and smaller species which are widely spread in Britain with a northern and sometimes a general holarctic distribution (e.g. *Agriolimax laevis*, *Vitrina pellucida*, *Hyalinia fulva*, *Hy. radiatula*, *Punctum pygmaeum*, *Cochlicopa lubrica*). Of the twenty species I have classed as calcicoles, eleven are absent and three rare in Scotland, nine absent and two rare in Ireland: of the forty-five indifferents, Scotland lacks three and Ireland six. The more widely distributed a mollusc, the less particular it seems about lime.

VII. GENERAL SUMMARY.

Our land Mollusca do not form specific associations with one another or with other animals or plants. Competition is therefore an unimportant factor. Their occurrences within their geographical ranges are determined by the conditions of the environment, the most important factors being moisture and lime. We may distinguish groups which affect wet places, dry places and human settlements. The rest, about half the species, live in ill-defined "woodland" habitats whose suitability varies in proportion to the shelter and lime they provide. In the alternative classification, we have one calcifuge species, about twenty calcicoles, about eighteen which prefer lime and some forty-five which are indifferent.

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THE RELICT METHOD IN DYNAMIC ECOLOGY

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(*With Plates I–V.*)

CONTENTS.

	PAGE
INTRODUCTION	39
Field methods	41
Material and objectives	42
METHOD OF RELICTS	42
Nature of relicts	42
Shrinkage of climaxes	44
Utilisation and interpretation	44
Supporting evidence	46
KINDS OF RELICT COMMUNITIES	47
Climatic relicts	48
Relicts due to human coactions	50
The trackway as a relict complex	51
The roadway as a relict complex	53
APPLICATION OF THE RELICT METHOD	54
Interpretation in the grassland climax	55
Short-grass proclimaxes	55
Bunch-grass prairies of California	56
True prairie	57
Interpretation in scrub climaxes	59
Sagebrush climax	59
Desert-scrub climax	60
Mesquite postclimax	61
Chaparral climax	62
Interpretation in forest climaxes	63
Deciduous forest climax	63
Coniferous climaxes	65
NATURAL AREAS AND RESEARCH RESERVES	67
REFERENCES	67

INTRODUCTION.

THE peculiar advantages offered by the continent of North America for the rise of dynamic ecology were recognised by Tansley nearly two decades ago (1916). These result not alone from its great extent in latitude, a feature that it shares with Asia, but also from the roughly parallel coast-lines and in particular the three far-flung cordilleras stretching from the Arctic to the

Tropics or Subtropics. Both coast and mountain introduce a regularity in variation without a rival elsewhere, and one that is unsurpassed in yielding values for comparison and contrast. Further striking features are the juxtaposition of the highest accessible mountain (14,500 ft.) and the deepest trough (396 ft. below sea-level) within 50 miles of each other, and mean rainfalls of 100 and of 1 inch within a few hundred miles.

As to the vegetation itself, the variety and extent of climaxes is unequalled, and the operation of glacial pulsations on these not to be matched outside of Europe. The great grassland formation is without a peer in its continuity and differentiation, and nowhere else is such a vast climax in contact with so many others of diverse character. Further, the deciduous forest of the East clothed a territory larger by far than that of eastern Asia, with a list of dominants quite beyond comparison. What is true of climaxes holds equally for climates, with the consequences that no other region of the globe possesses such an opportunity for tracing the causal relation between the two.

Turning to dynamic features, North America is not surpassed in the number of lakes and mountain ranges that afford bare areas for hydrosere and xerosere. Even more characteristic is the number of coastal, river, and inland dune areas, and the wide extent of "bad-lands." However, it is in connection with secondary succession that this continent stands pre-eminent. This is due in part to the features already enumerated, but chiefly to the fact that it occupies a median position between Eurasia and the austral continents with respect to its conquest by man. The latter has not been in possession sufficiently long to have modified profoundly the natural vegetation, as in Europe and much of Asia, and yet his influence has been more marked and extensive than over most of the area of other continents. Even more significant has been the wave-like migration of population to the westward, with the result that man and his processes have left a graduated record of the changes wrought, a scale of effects of the first importance to dynamic ecology.

The first contact with the outstanding changes of North American vegetation revealed the significance of drought periods and overgrazing for the interpretation of the structure of grassland, in the course of a 200 mile reconnaissance along the Missouri and Niobrara rivers in Nebraska (Clements, 1893). Similar expeditions further to the west at the end of the protracted drought, in 1896–8 (cf. Shear, 1901), confirmed the significance of the dynamic approach, and this was embodied in the first treatise on this theme (*Fundamental Principles of Vegetation*, 1901). Since this time, the dynamic method has been developed in great detail and tested year after year in the widest range of vegetation. Certain major features of it have been made available from time to time (*Research Methods*, 1905; *Plant Succession*, 1916; *Plant Indicators*, 1920), but a comprehensive and usable account of the detailed technique has awaited the present occasion (cf. *Carnegie Institution Year Books*, **16–31**, 1918–32).

With development as the key to vegetation and later to the biome, it became obvious that a study of the actual community at a particular time and place could yield only a static picture. Though a knowledge of "what is on the ground" is both indispensable and prerequisite, by itself it represents but a segment of the dynamic flow of processes. Taken alone, its facts are deficient in meaning or actually misleading, and it is solely by placing them in the proper setting as to time and events that they gain their true significance. With vegetation as with life in general, it is an axiom that the present is the heir to the past and the forerunner of the future, but an axiom that lies at the very foundation of ecology. This is merely a figurative expression of the principle that causes produce effects and these in turn may become causes, the cardinal tenet of ecology by virtue of its very name. In brief, the understanding of existing vegetation cannot proceed out of itself alone, and one must turn to causes and processes for its interpretation, as well as to forecast the course of its future development or its fate.

Field methods.

Ecological methods for the field fall into four major categories, namely: (1) measurement by means of instrument, phytometer and quadrat; (2) development, community functions and especially the complex process succession; (3) experiment in terms of exclosures, transplants and field controls, and (4) indicators, which contain values derived from all of these in terms of nature's experiments. The present treatment is concerned directly with the last and through this with all the others, since it lends itself readily to observation and reconnaissance. However, the method of indicators must be on the one hand fully synthetic and on the other both detailed and comprehensive to yield objective results of permanent value. It cannot be applied with safety or accuracy to a local area alone, nor can it transmute the observations of hasty reconnaissance into dependable results. As always in ecological studies, the extensive must be refined by the intensive, and the latter in turn carried into other areas and regions to secure adequate tests of its general trustworthiness. Thus, in the researches of the past forty years, intensive work has been carried on at four bases, Lincoln, Pikes Peak, Tucson and Santa Barbara, while approximately half-a-million miles have been travelled in the course of reconnaissance, with the consequence that many regions have been studied again and again.

The repetition involved is an indispensable feature of thoroughgoing field technique, by virtue of three major reasons. The first is that it permits examining each community in the entire round of the seasons, a matter of the first importance for studying the dominants and subdominants of grassland in particular, many of which are visible and important only during the proper aspect. The second and even more significant is the striking difference from year to year in consequence of the effect of plus and minus phases of the climatic cycle, as exemplified in the process of annuation. For example, when first visited in 1893 at a time of sunspot maximum and drought, the grassland of the Niobrara region was composed chiefly of short-grasses; at a later visit in 1915, a period of sunspot minimum and excessive rainfall, these were entirely secondary to the mid-grasses of the mixed prairie. A third reason, of especial import in the present connection, is the progressive nature of man's coactions upon vegetation and fauna, often complicated by the cessation of a particular activity and process, or even by its reversal. Most significant of all is the fact that the interaction of all these climatic and human processes imparts to the biome a quasi-experimental value that is often not to be matched by actual experiments. Such natural examples are so numerous and varied as to constitute incomparable material for comparison and interpretation.

Materials and objectives.

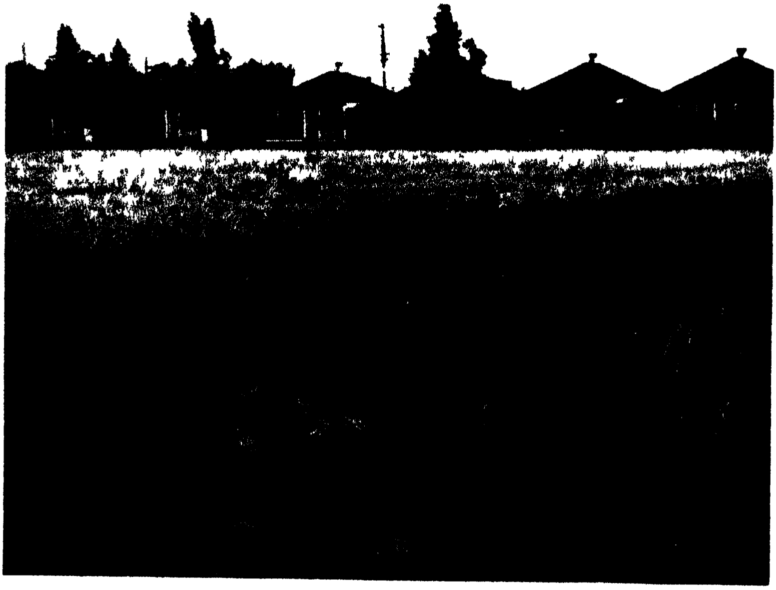
The indicator method and its applications have been discussed in comprehensive fashion in *Plant Indicators* (1920) and *Plant Succession and Indicators* (1928), and it will suffice to point out here merely the general relations. Dominant and subdominant, climax and sere in both structure and development, all are eloquent indicators of factor or process, and hence of past events and of future changes in the biome. The basic relation is that of the species-individual or specient to its habitat, and all indicator values are derived in the last analysis from the closeness of this bond. It explains the orderly progression of succession under the control of climate, as well as deviations from it, and also the temporary or permanent modifications due to climatic pulsations. It is the indicators of physical factors in terms of climate and soil, of water, heat, light, solutes, etc., and of such complexes as altitude, slope exposure, and erosion that serve as the basis for unravelling the various functions of the community, such as reaction, competition, coaction, and the many processes by which man in particular modifies it, by virtue of burning, clearing, cultivating, fencing, grazing, or draining. For the present purpose, these fall into two major groups, namely, climatic indicators such as preclimax, postclimax and clisere, and edaphic ones of disturbance, viz. proclimax, subclimax, and subsere especially. However, all these have in common the fact that they owe their significance to their position in a cause-effect sequence leading from the past to the present and forward into the future.

METHOD OF RELICTS.

Nature of relicts.

In the ecological sense, a relict is a community or fragment of one that has survived some important change, often to become in appearance an integral part of the existing vegetation (Clements, 1920, 1922). Thus, the hemlock (*Tsuga canadensis*) constitutes relict groups in the maple-beech forest of the eastern United States; the tall Andropogons are relicts in the sandhills of

Phot 1 Climatic relicts of *Hilaria Stipa Aristida* and *Oryzopsis* on rocky slopes, Death Valley, California.



Phot. 2 Relict area of *Stipa comata* consociation, suburbs of Colorado Springs, Colorado

CLEMENTS—Relict Method in Dynamic Ecology

Nebraska, and the grasses bear a similar relation to the desert scrub of Death Valley. Obviously, the term may be applied also with equal warrant to the individual or the species, but it is a practically universal rule that a community of some degree is concerned. Though it may be employed properly for laggards in the course of succession, its most significant use is in connection with climaxes and these naturally furnish the most striking examples of it.

It is evident that relicts possess two indicator values of the first importance. These relate to the causes concerned on the one hand and to the original vegetation and its changes on the other. The former may be climatic, edaphic, or human, each exhibiting a more or less distinctive impress. Climatic causes operate primarily upon the climax, with the widespread destruction of the existing community and the mass migration of the complementary one as the outstanding effects, illustrated by the replacement of grass by scrub in the Mohave Desert (Pl. I, Phot. 1). Edaphic causes are expressed largely in succession, relicts being conspicuous only when the denuding process is more or less partial. Human agencies are characteristically destructive and their operation is naturally most frequent over the wide stretches of climax, or subclimax after these are once established. The consequent relicts occur and recur in endless number, and supply an unlimited opportunity for the investigation of natural experiments in development.

In accordance with the preceding, the presence of a relict community indicates the operation of a compensatory or protective feature. In the case of a dry phase of the climatic cycle, the compensation for reduced rainfall may be provided by altitude, by northerly slope exposure or a sandy soil. With new or denuded areas, the determining feature may be elevation or a barrier, as in flooding or lava flows, the location of channels in the case of draining, or the force and direction of the wind, as exemplified by the drifting of dune sand or the running of fire. The relicts due to human agency, directly or indirectly, are consequences of protection in various forms, except for the rarest instances. Such protection may be purposeful, but in the newer continents especially it is chiefly accidental, involving the widest range of choice and object. Conservation in fact is primarily a change from the accidental to the intentional protection of communities; in other words it is chiefly the preservation and extension of relicts. Protection assumes a variety of forms, of which fencing and fire lines are the most universal, though it is not infrequently inherent in plant or group. However, it is obvious that protection by fencing applies only to exclosure, since enclosure in varying degree may lead to profound modification, or even to complete destruction in corrals.

The location of relicts will be largely determined by the process concerned. Climatic relicts are typical of the ecotones between formations or associations, and in particular of dissected regions along the front of broad movements. They also occur not infrequently in the heart of great climax areas, where outlier, canyon, or sand provides the necessary compensation. Relicts due to man's activities follow or reflect more or less closely the location and frequency of the latter. Forest relicts mark the course of lumbering and fire, those produced by cultivation characterise farming regions, and those consequent upon grazing are to be chiefly found in peripheral grasslands, while the effects of construction are usually localised about cities, towns, and highways.

Shrinkage of climaxes.

The special study of relict communities in North America for nearly two decades has led to the conclusion that effective migration is by climax masses under the compulsion of climatic changes (Clements, 1922, 1925, 1931), and this has been reinforced by the experimental study of ecesis and competition in different associations (*Experimental Vegetation*, 1924; *Plant Competition*, 1929). As a corollary of this, shrinkage comes to be seen as a dynamic process, typical of the phases of desiccation so characteristic of western North America. It is evident that these brought about such migrations as that of the prairie climax into the forest and of desert scrub into grassland. However, such advances were contingent upon climate throwing the balance in competition for water to the side of grasses and against trees, and this meant the slow destruction and consequent elimination of forest, through three fairly well-defined stages. The first was the dropping out of the more mesophytic species, the second a withdrawal from the finer soils of the general level with a high echard, leaving the more xeric species in valley, on mountain ridges or in sandy soils. and the third the death of older and weaker individuals under the increasing competition of the grasses, resulting in the production of savannah.

A fourth consequence was the dwarfing of the individual trees, producing a unique series of climatic indicators, such as those of Oklahoma in which the dwarf oak or "shinry" of the western sandhills persists as the rearguard of the fine climax forest of the Ozark Plateau, the stragglers between increasing in height and density toward the latter. Shrinkage under the same climatic pulsations has produced the more extensive oak savannahs or "Cross Timbers" of Texas in the long sandy inclusions of the "black-land" prairies.

Utilisation and interpretation.

At the outset extensive and repeated survey is essential to disclose the largest possible number of relict communities of any particular type. This is important not merely to determine the area concerned, but especially also to reveal the degree of harmony between the various examples. Disagreement between some of these is often a source of new leads and frequently demands re-examination during other seasons and years. In most cases, such disagreement is merely superficial and disappears on the more thorough analysis afforded by comparison. It is clear that harmony can be expected only between relicts of the same type and due to the same cause, though in any particular climax there will be a certain degree of relation between relicts of different types.

Interpretation is a relatively simple procedure, which deals in each instance with the cause as the clue to what has transpired in the past and may be expected in the future. However, it takes quite a different course in the case of climatic relicts than in those produced by the coactions of man and animals. In the former, it is based upon the clisere or series of climaxes that reflect increasing altitude and latitude on mountain chains or on continents. This is the sequence of communities that is moved back and forth by the phases of a major cycle, leaving relicts in all situations that possess proper compensation against the new climate. In the case of the great coactions, such as fire, clearing and grazing, the process itself supplies the key to unlock the meaning of relicts, but the actual analysis must reckon with response to the changed factors, with reaction upon the habitat and the competitive equipment of the species concerned. Such analysis in typical instances is discussed with some detail in a succeeding section.

Since the clisere indicates the basic climatic relation of climaxes, it provides the most illuminating interpretation of such relicts. The bond between the included climaxes is well expressed in the statement that these move concomitantly with the shift of climate and that each bears a reciprocal ecological and topographical relation to the other. These inter-relations have been crystallised in the terms preclimax and postclimax (Clements, 1916, 1928; Weaver and Clements, 1929). In the static clisere of a great cordillera, such as the Rocky Mountains, the preclimax of the montane forest is the xeric mixed prairie at the base, and the postclimax, the more mesic subalpine forest at the higher altitudes. In periods of mass migration, the prairie is preclimax to the forest and the latter postclimax to the prairie, a relation discoverable at any time in the ecotone between them. Arctic tundra is preclimax to boreal forest, alpine tundra to subalpine forest; grassland is preclimax to scrub and forest formations, while these are typically postclimax to it. The same general principle holds for the associations of a formation, mixed prairie being preclimax to true, this postclimax to the former; maple-beech is postclimax to oak-hickory, and the reverse, while hemlock is postclimax to maple-beech.

The term subclimax has been purposely employed for two somewhat different concepts since its first proposal (*Plant Succession*, 1916) to permit economy of terms until the need for closer definition became more generally recognised. A recent discussion of this matter by Godwin (1929) and by Tansley (1929) indicates that such may now be the case, and in consequence it is proposed to restrict subclimax to an actual subfinal stage in the sere. For those cases in which the community is modified and held for a more or less indefinite period in some other condition, as with the short-grass plains of North America, the term "proclimax" is suggested. Since grazing, clearing and fire regularly exert a selective action, the majority of the communities heretofore called subclimaxes will now become proclimaxes. However, it must be recognised that our present knowledge of development will not always permit an exact distinction between the two, and furthermore that proclimaxes are not all identical in character.

Supporting evidence.

It is obvious that interpretation on the basis of observation gains much from other methods when these are applicable. The primary canon of ecology is synthesis, in accordance with which it is imperative to utilise all the sources of supporting evidence. Though of various kinds, these may be comprised in four main categories, namely, (1) relations still existing in the climax, (2) records, (3) cycles as natural experiments, (4) experiment, especially in the form of closures. Constant attention has been paid to all of these during the period of relict studies and a large amount of material has been accumulated, the bulk of which must be left for detailed consideration in the future. Here it must suffice to suggest the methods and to assign to each its proper place in the synthetic pattern.

Although such great climaxes of North America as the deciduous forest and the prairie have been profoundly modified and fragmented over most of their respective regions, there are still areas in which the original relations of the dominants obtain, especially in the grassland. By utilising these as a standard for comparison, practically all degrees of change may be evaluated objectively and the task of interpretation greatly facilitated. During the period of these investigations, such correlations have been frequently established with relicts that were later destroyed, thus producing conditions identical with those in which relicts had disappeared too early for record and imparting to the course of events a certainty otherwise impossible of attainment. Of much the same nature and importance is the effect of annuation in response to changing phases of cycles. Wet seasons on the Great Plains, by increasing water content and decreasing competition, have regularly reproduced in convincing fashion the mixed prairie in wide stretches that are apparently short-grass climax during dry years. In the south-west, such periods have restored the grass dominants to a degree that leaves little for experiment in demonstrating that the *Larrea* community really constitutes a savannah in the desert-plains grassland.

In the field of human documents, there are three chief categories to be considered, though these grade more or less into each other, namely: (1) scientific records, (2) exploring and surveying records, and (3) records and recollections of pioneers. The latter may be dismissed more or less completely at the outset, since they only have value in the exceptional cases where the settler possessed definite botanical knowledge. The same treatment applies to the boyhood recollections of naturalists and botanists, the most illuminating instance being that of a writer who speaks of being "intimately acquainted with the prairies since the year 1871," at which time he was five years old.

The weight to be assigned records of exploration depends upon whether the personnel contained botanists or men with some technical knowledge of the plants, the myth of the "Great American Desert" being largely a tribute to the powers of observation of the layman. In forested regions, the logs of surveyors often possess values in detail, as Sears (1926) and others have shown. Finally, the records of scientists are naturally of the first importance, those of Bessey and his students in Nebraska and of the United States Division of Agrostology in the West generally, made from 1885 to 1900, being a mine of information for tracing changes in grassland.

After all the evidence indicated has been secured, the last element of certainty must be contributed by experiment. This is fairly simple in the case of grassland, more difficult with scrub and still more so with forest. The effect of fencing upon conservation and especially in promoting recovery was noted as soon as attention was turned to the theme of relict communities, and led logically to the extensive installations of exclosures and enclosures made in Arizona in 1918 (Clements, 1918, 1920). These and others in various associations have not only furnished decisive demonstration of the relation of relict to climax, but also revealed the rôle of stock and rodents in the process of modification.

The influence of climatic cycles in terms of annual variations in density and volume is measured by means of isolation transects, consisting of central strips permanently protected against cattle and against cattle and rodents, units being exclosed and enclosed each year to furnish a graduated annual scale of effects. In addition, series of small plots a few metres in area are installed to determine the effect of various processes, such as denuding, burning, clipping, sowing, planting, removal of grasses or forbs to measure competition, and so forth. Experimental exclosures of various types have been established for a decade or more in all the grassland associations and have confirmed the original field interpretations in every case.

KINDS OF RELICT COMMUNITIES.

As indicated previously, relict communities fall into two well-defined major groups, viz. those due to climatic pulsations and those produced by human coactions. Relicts of the first type owe their persistence to some compensating action of topography or soil, typically upon the holard, while the second type derives from protection in some form, usually as fencing. In a few cases, the same feature will exert both effects; thus a rocky slope or ridge will afford refuge to trees or shrubs by virtue of reduced competition and, at the same time, by reason of its steepness and uncertain footing protect grasses from overgrazing.

The variety of relict areas is so great that it is impossible within the scope of a paper to give detailed treatment to all of them. In consequence, they are here passed in review with a brief mention of their salient features, while a few of the most important types are given more extended treatment.

Climatic relicts.

By far the greater majority of these are due to the compensation afforded by topographic features, such as altitude, slope exposure, ridges, or valleys. The compensation provided by altitude operates chiefly upon water content through increased rainfall and decreased temperature, but it bears also a more or less definite relation to evaporation and transpiration. However, the difference in altitude must be neither too small nor too great; in the one case, it is insufficient to produce perceptible effects, and in the other it leads to the presence of a distinct climax. Elevation in terms of land forms is expressed in hill, ridge and mountain, characterised by striking differences in exposure to insolation, due partly to period of reception, partly to angle of slope, and partly also to shadow. The effective difference between northerly and southerly exposures is again one of holard and transpiration primarily, with certain secondary effects of temperature (Clements and Lutjeharms, 1922).

The cooler moister slopes have been termed mesoclines, and the warmer drier ones, xeroclines, between which lie areas of smaller differences. The mesocline is regularly postclimax to the level plain, and the xerocline preclimax to it, while they bear a somewhat similar relation to each other. In periods of desiccation, the mesic communities shrink to the point of disappearance, first on the south-west, then south and finally south-east, usually making their last stand on north-east slopes; during wet intervals, the mesocline spreads to the south-east and south, but rarely invades the south-west slope. This relation holds true for all three major climaxes, forest, scrub and grassland, but naturally attains the most striking expression where two of these are concerned. In addition to the major features are innumerable finer details of value and interest, the presence or composition of consociation or society shifting with small variations in angle of slope, exposure, surface, texture, or soil profile.

The seration, or sequence of communities across valleys, exhibits similar though inverted relations in comparison with the ecocline, by virtue of its concave form. The movement of run-off into the centre of the valley, as well as cold-air drainage, determines this as the area of compensation, which is usually emphasised by the presence of a stream. Consequently, shrinkage proceeds from the walls inward, the characteristic fringing forests of prairie valleys being postclimax to the surrounding grassland. The walls or bluffs themselves present conditions closely resembling the two ecoclines of a hill, but the south wall has a north slope exposure and hence is a mesocline, while the northerly one with southern insolation is the xerocline. As with ridge and mountain, the valley exhibits minor relief in terms of breaks, ravines, vales, knolls, etc., with corresponding variation in the composition and persistence of relicts.

The understanding of climaxes and the interpretation of relicts is advanced by recognition of the fact that the clisere of a major mountain range, the ecoclines of a hill or peak and the series of communities across a valley bear much the same relation to climatic cycles. There is the same essential bond between the climaxes or climax relicts in terms of potential movement or of succession, of expansion and contraction, whether this be up and down the mountain slope, around a hill, or back and forth across a valley. By the careful comparison of all three in a particular region, it is possible to secure a long look backward into the past and forward into the future of the biome.

Probably the most dramatic, as certainly heretofore the most puzzling, compensation for desiccation has been that afforded by sand hills and sand plains. This is because the compensating factor, the soil texture, is not at once visible and the correlation of the great relict communities with a definite cause is far from evident. Such relations are to be found in sand or gravel soils everywhere, especially in ecotones, but the most striking and best-known cases are probably those of the sand hills of Nebraska and of the sand plains and river dunes of Texas and Oklahoma. The former are characterised by a tall-grass postclimax in the midst of climatic mixed prairie, and the latter by extensive relicts of the former oak-hickory association that has shrunken into areas enclosed by coastal or by true prairie on "black-land." The preservation of the original climax in the form of a postclimax is due in both cases to the same type of compensation, namely, the higher echard of sand by contrast with loam and the effect of the sand upon absorption and run-off. However, in the course of centuries or millennia, this advantage is gradually lost by the decay of organic material, the sand becomes finer and the echard rises, with the result that the forest first becomes savannah and is then more and more open, to the point of disappearance in the grassland. In the reciprocal climatic phase, the forest would encroach upon the grassland of the fine soils owing to the rise of the holard in conformity with increasing rainfall, but the spiral-cyclic movement toward desiccation in North America since the Cretaceous permits few if any relicts of this type, at least outside regions of major glaciation.

As suggested earlier, the series of forest relicts extending through three prairie associations from New Mexico to Missouri affords a remarkable opportunity for their correlation—one perhaps unparalleled anywhere in the world. The westernmost relict is one of *Quercus muhlenbergi* in a deep canyon of the Capitan Mountains in New Mexico. On the sandy plains of eastern New Mexico and western Oklahoma, *Q. stellata* and other oaks are represented in the dwarf "shinry," at the extreme only a foot high. Caddo Canyon and other deep narrow gorges of central-western Oklahoma still harbour relict forests of deciduous trees, in which *Acer saccharum* may be the chief dominant. Further east, oak-hickory relicts fringe the streams and persist as savannah on the ridges. Along the eastern border of the state, the massive outliers of the Ozark Plateau are covered with dense savannah of tall trees, and on the

Plateau itself this passes into oak-hickory climax, with postclimax maple in the deeper valleys and rarer relicts of beech.

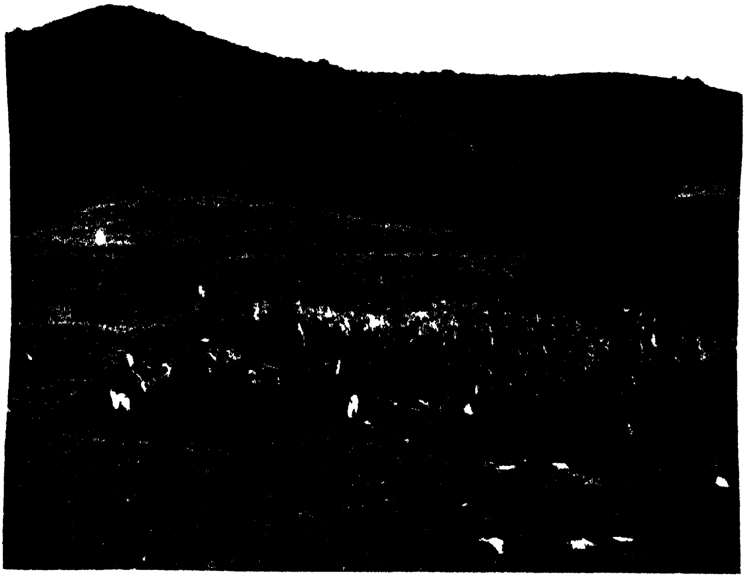
Relicts due to human coactions.

While these are all a consequence of the operations of man, his action is an indirect one in the case of grazing especially. In practically all cases, the compensating factor is protection, though this assumes quite different forms, from such physical barriers as fences at one end to moral or legal restraints at the other. Obviously, the overwhelming number of coaction relicts are the result of fencing, and the others serve chiefly to attest the principle. Quite as clearly, it is "fencing-out" or exclosure that counts in the conservation of relicts, since overstocking and consequent overgrazing of fenced pastures and ranges have caused universal modification of the original climax.

In actual practice, fencing bears no such relation to forest as it does to grassland. The general effect of clearing and lumbering has been to destroy the forest, to the extent that virgin relicts persisted only in inaccessible regions or in tracts of little or no economic importance. On the other hand, fire, intentional or otherwise, has known no restraint until the era of conservation, with the consequence that virgin forests are all but unknown between boreal and tropical regions. However, the sprouting faculty of deciduous trees has counterbalanced lumbering and fire in large measure, and extensive relicts in the form of "second-growth" are to be found throughout the deciduous climax. In the case of some conifers, the general absence of sprouting has been offset by the resistance of thick bark as in *Pinus ponderosa*, or the peculiar equipment of the seedling as in *P. palustris*, and even more by the vagaries of wind, weather, or terrain in modifying the course of fires and leaving relicts. As in other respects, scrub falls in between grassland and forest, inasmuch as it readily forms root sprouts, with a few notable exceptions like sagebrush, but often requires protection from browsing.

Because of their frequence, continuity and the relatively early date at which they were fenced, railroad rights-of-way surpass every other source of relicts in the Middle West and Far West. For much the same reasons, roadways come next in importance, though the fencing of the adjacent fields and pastures is less regular and often more recent. Both present a myriad of relicts under the whole range of climax conditions and structures, and for this reason in particular their analysis is carried out in some detail. Fencing in other forms likewise leads to the preservation of relicts, as in the corners of fields, between fence and field-edge, in cemeteries, rural schoolyards, many farmyards, and so forth. An indirect effect of fencing is seen in the immunity of hay lands from grazing, and this often extends also to unfenced roads and railways. A similar consequence occurs in the twilight zone between town and country, where in grazing regions some of the best relicts are to be found by virtue of custom or actual regulation (Pl. I, Phot. 2). Vacant lots in cities

Phot 3 Mixed prairie protected from grazing by precipitous canyon walls, Big Bad Lands, Sheep Mountain, South Dakota



Phot 4 Relict *Stipa pulchra* protected by *Opuntia* in overgrazed pasture, Banning, California

frequently exhibit areas of the original grassland practically unchanged, and some relicts of this type are known to be fifty to a hundred years old.

In the case of reservations and reserves set aside by law, the areas are generally the most extensive of all, but their value as relicts is determined in large measure by their age and type of utilisation. The Indian reservations are the oldest of these and they afford unsurpassed examples of climax grassland when leasing has not permitted overgrazing. National parks and national forests are usually of a later date, but intelligent conservation in both and the actual regeneration of the range in the latter give great and growing value to these as sources of relicts. Most valuable of all, however, are such grazing ranges as the Santa Rita Reserve in Arizona, the Jornada in New Mexico, and the Wichita in Oklahoma, in which utilisation under proper regulation is supplemented by exclosure and other experiments. In the case of game preserves and refuges, and state parks, relict values are sometimes secured, but too often the lack of regulation and the kind of popular utilisation have no effect other than to render them object lessons.

Other types of protection that produce relict communities are an outcome of barriers of various sorts. Precipitous slopes and abrupt canyons prevent the access of stock more or less completely, as in the classic example of Sheep Mountain (Pl. II, Phot. 3), and this effect is sometimes produced by swift streams. A district without surface water rarely permits utilisation of the grass, and such areas are to-day practically unchanged by coaction. Even on a cattle range, distance to water determines the degree of grazing and the more remote portions are usually much less utilized. Finally, cacti, bushes with spines or thorns, or with dense stiff branches regularly serve to protect the grasses growing in or near them, sometimes providing the sole evidence of the former grassland over extensive areas (Pl. II, Phot. 4).

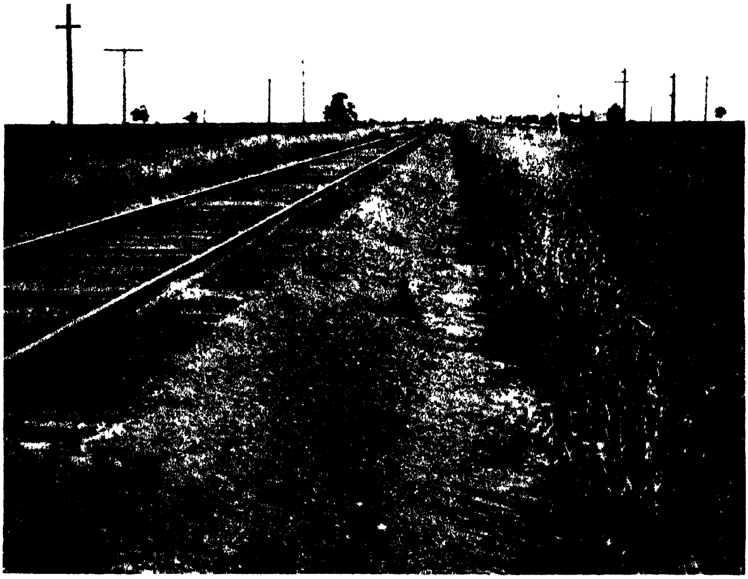
Some types of soil provide a certain amount of compensation for coactions, in something of the manner they do for climatic changes. Sand, by virtue of its large amount of available water, regularly affords a refuge from overgrazing, to the extent that the plants grow more vigorously, especially in dry seasons, and the competition for water is less than in hard soils. A pebbly or flaky soil has something of the same effect, though the reduced cover is the chief feature in maintaining a better water content. A rocky terrain also offers handicaps to a good footing, as well as to actual grazing, especially when the rocks are upthrust in ridges, and the ecologist in search of relict grasses and forbs rarely inspects such an area in vain.

The trackway as a relict complex.

The value of a right-of-way as a relict area depends primarily upon its age and upon fencing. The latter has significant effects only in the grassland climax, or rarely in scrub. The fence must have been installed at the time of construction or at least not so long after as to permit serious modification, and must have been well maintained. Trackways without fences or with these broken or later removed are not to be ignored, but the evidence obtained from them must be scanned in the light of fenced railways in the same district. In the case of those long established in populous regions, disturbances of all sorts have occurred to replace the natural grassland with ruderals, while railroads of recent construction are usually laid down in a cover already much modified.

More and more are rights-of-way mown and even grazed, burned each year, or utilised for cropping, as was especially the case during the war period of 1917–18. In addition, the cover has been much changed in consequence of the disturbance resulting from construction, in the form of road bed, cuts, fills, dumps, and ditches. As a result, nearly every trackway is a mosaic of climax and seral communities, especially of the subsere. The distinction between these is rarely attended with doubt when made on the basis of indicators alone, but this can always be confirmed by the nature of the terrain itself. Through rolling prairie and sand hills, the trackway is an endless succession of serations, of swale or valley, level, and hillock or hill; the vales are regularly postclimax or seral in character, the levels climax for the most part, as are the hills also, except when they are low enough to permit the dumping of material on the tops. On plains, the climax was formerly continuous for the most part, but this has sometimes been modified for long distances by severe burning and not infrequently by ploughing (Pl. III, Phot. 5).

Transversely, a trackway consists of two sets of parallel zones, one on each side of the road bed. These both change from lowland to level and to hillock depending upon the manner and degree of removing the soil, and they sometimes differ from each other when bordered by a road or by different kinds of cultural and native vegetation. The road bed, where built up, is the site of weedy subseres in all stages unless it is ballasted or oiled, though the weeds are often cut or burned each year. When the bed lies on a high fill, the slopes of the latter permit the development of larger ruderal associes and these often lead to some phase of climax or subclimax, when the trench at the base is not too deep and wet. If the latter is broad and shallow, it is the site of postclimax species, for example tall-grasses in both true and mixed prairie, and differs little from the postclimax vales. This ditch is usually excavated from the climax level, which is typically covered with the original grassland, with allowances for the various disturbances already mentioned. At the fence line, the level is often modified by the invasion of ruderals from roadside or field, or by the cropping of itinerant horses or cattle. In the case of cuts, both the road bed and slopes are poorly colonised, unless the latter are sufficiently oblique to permit invasion from above. When the excavated dirt is piled on the original hillock, a short ruderal subsere ensues, soon followed by invaders from the climax and this is sooner or later reconstituted. Cuts are often protected by snow breaks that by virtue of drifting snow and summer shading bring about certain changes, but usually well within the climax range.



Phot. 5. Relict bunch-grass prairie in trackway,
San Joaquin Valley, California.

Phot. 6. Relict *Stipa*, *Poa* and *Melica* on roadway shelf
above deep cut, Paso Robles, California.

The roadway as a relict complex.

As a result of greater variety of type, roadways often furnish a wider range of evidence than trackways, though the relict areas are smaller and less continuous, owing to constant disturbance and readier invasion. The relict strip between road bed and fence is rapidly being eliminated along main motor highways, especially by successive widening, but it will persist for a long time on secondary ones and still longer on country roads and trails. Roadways naturally resemble trackways in the seration features of valley, level and hill and increasingly so in the provision of deeper cuts and fills; they are likewise characterised by parallel strips on either side of the bed.

Except on surfaced roads, the roadside is usually occupied by decumbent ruderals held in an initial stage of the subsere by packing. This slopes gently to a ditch often flooded and hence occupied more or less permanently by tall annuals and perennials. Above this rises vertically the road shelf, which is regularly little affected by road making and bears a more or less continuous cover of relicts. These may extend into the field strip inside the usual barb-wire fence, may lose themselves in the modified cover of pasture or range, or continue into schoolyard, farmyard or cemetery. The wire fence rarely exerts any distinct effect upon the relicts, but rail and board fence and hedges frequently conserve relicts by reducing evaporation and transpiration and increasing the holard through foliage drip.

Since road shelf and field strip are protected from all but sporadic grazing, the persistence of relicts in them is largely determined by the invasion of ruderals and the consequent competition. Both field and experimental evidence demonstrate that weeds quickly yield to native grasses when invasions are single or infrequent, but the recurrent and increasing pressure of weeds finally causes the disappearance of grass. The outcome is chiefly determined by the ease with which the seeds of weeds reach the relict areas. When the shelf is low and the adjacent field weedy, invasion and competition are at a premium and the strip becomes dominated by a short and persistent subsere. If the shelf is high, the chances of the relicts are greatly improved, especially in front of a pasture rather than a tilled field. The shelves of deep cuts are best protected from invasion from the road and, since such country is generally used for grazing rather than crops, almost equally well from the other side. In consequence, the shelves of such cuts are standard refuges for relict grasses, especially in California where they have been crowded out in all the lower intervals by the introduced annual grasses (Pl. III, Phot. 6).

From such shelves, grasses and forbs, especially *Stipa*, colonise the slopes, and this has sometimes given rise to the erroneous impression that *Stipa* has "come in" from some vague source. However, in practically all such cases, the original climax group still persists above, to leave no doubt of the actual process. When a road shelf a few feet high is paralleled by the ditch, as is regularly the case, the edge is often marked by a taller and denser growth of grass relicts; this is due partly to reduced competition at the ditch. Such edges and ditches also serve as easy pathways for alternating migration and ecesis of tall-grasses from the lowlands, and thus explain in part the gradual encroachment of these upon the mid-grasses of slope and upland in both true and mixed prairie.

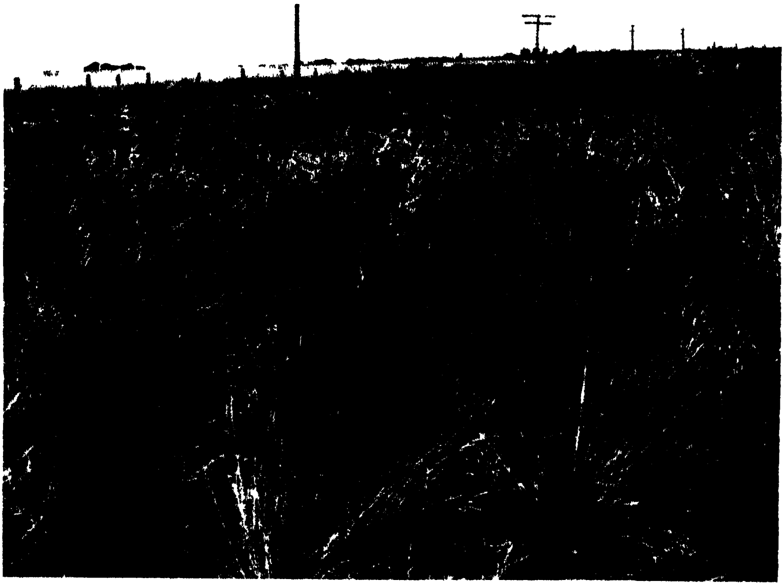
From the preceding, it becomes evident that trackways and roadways furnish an amount and variety of evidence as to the course of modification and manner of control of grassland that cannot be matched elsewhere. No adequate and accurate understanding of the climax is possible without taking these into account; as a field procedure they warrant more attention than is given other relicts because they permit the ecologist to use interpretation with a certainty and detail otherwise impossible. This is well illustrated by the remark of a colleague on a field trip through the prairie, to the effect that he was finally beginning to understand why at each stop a visit was first made to the trackway before going to examine pasture or open range.

APPLICATION OF THE RELICT METHOD.

In applying the relict method to the interpretation of a particular climax, it is important to realise at the outset that the structure of the latter is a mosaic of climatic, seral, and coactive effects. The initial task is to distinguish these on the basis of both cause and process and thus disclose their interrelations. This is a fairly simple matter in the case of priseres and subseres, since the sequence of stages is more or less evident, but it demands a wider survey extending through several years to recognise the various climatic indicators. When these consist of a typical portion of the association or of its subdivision, the faciation, the nature and relationship of the relict are usually evident, but this is less true of the consociation, consisting of a single dominant. However, in such cases, the clue is furnished by the rule that dominants, like associations, arrange themselves in more or less definite sequence, the reciprocal relation between them being maintained under practically all changes of climate. The test of this is afforded by the plus and minus phases of the climatic cycle, and hence the study of the responses of both climax and relict to such extremes is indispensable to proper interpretation. In western North America, the amount of rainfall at the sunspot minimum may be three to four times greater than at the maximum, and the potential changes of the climax may approximate those of a major climatic pulsation.

Coaction is so widespread and recurrent that its major consequences are often readily recognised. However, in the case of relicts, the process may be no longer in effect, its operation may be obscure, or it may be complicated by the concomitant action of other processes. In consequence, it becomes necessary to read the evidence in the light of each type of coaction in actual operation, and finally to appeal to experiment for a conclusive judgment

Phot 7. Regeneration of tall-grass from short-grass in 5 months by fencing, Wichita National Forest, Oklahoma.



Phot. 8. *Stipa pulchra* consociation of San Joaquin Valley as seen in trackway, Fresno, California, 1918.

CLEMENTS—RELICT METHOD IN DYNAMIC ECOLOGY

Face p. 55

(Clements, 1910). While fire and lumbering, for example, have very obvious effects, these relate chiefly to destruction, and the detailed course of the coaction is but little understood. This applies with especial force to coactions in grassland and in scrub, where the procedure is more obscure or at least less conspicuous. The selective action of burning is probably decisive in the large majority of cases, and mowing, usually regarded as of little or no influence, usually produces a distinct and sometimes a pronounced effect. Hence, in the interpretation of relicts, a synthetic approach in the light of all the evidence, supporting as well as indicator, negative as well as positive, is imperative if objective values are to be secured.

Interpretation in the grassland climax.

The value of the relict method for interpreting the present structure of the grassland climax and retracing the changes concerned may be illustrated by three outstanding problems in it. These are the origin and significance of the short-grass proclimax, the original dominants of the California prairies, now generally replaced by annual grasses, and the invasion of bluestem and bluegrass into the eastern true prairie, at the expense of the mid-grass dominants. Before this method was called into requisition, it was inevitable that the community in possession should be regarded as climax, except in California where the native forerunners of the annuals were unknown. This was the view embodied in the *Phytogeography of Nebraska* (1898) and generally adopted for two decades, until comparative studies of the several grassland associations in the light of climatic cycles and human coactions led to its modification (Clements, 1919, 1920).

Short-grass proclimaxes. By far the most extensive and best known of these is the short-grass community of the Great Plains, stretching through the mixed prairie from Saskatchewan to Texas. However, the essential relations for the production of such a proclimax exist wherever short and tall grasses occur together and are subjected to overgrazing. This is notably the case with mat-formers such as *Buchloë dactyloides*, *Hilaria cenchroides* and *Cynodon*; together with several species of *Bouteloua* one or more of these regularly replace mid-grasses and tall-grasses in true, coastal and subclimax prairie under intensive grazing in pastures (Pl. IV, Phot. 7).

The first intimation that the short-grass plains were not a climax in the climatic sense was obtained during the summer of 1915; this was a season of excessive rainfall coinciding with the lowest sunspot minimum known for a century. The mid-grasses appeared abundantly in the cover of short-grass and in many places obscured the latter more or less completely. Since these were all perennials, it was obvious that they could not be regarded as recent invaders but must have been present in the community in less conspicuous form. This led to a search for protected areas in which they retained much of their normal importance and resulted in finding such relicts in a wide variety of situations. The protection afforded against grazing by fences usually supplied the most striking examples, as in the case of trackways, reserves and cemeteries especially, but sandy soil and rocky slopes regularly yielded mid-grass dominants. This explanation was supported by the course of events leading up to the drought period of 1917–18, when the taller grasses diminished in height, failed to produce flower stalks and became relatively inconspicuous in the dense short-grass sod. A similar fluctuation was found in succeeding cycles of dry and wet years without exception, and this effect can now be traced in the accounts of various expeditions, the discordant opinions of the "Great American Desert" being readily harmonised on the basis of the sunspot cycle in relation to rainfall.

During the intervening period, many thousand relicts of all sorts have been recorded throughout the mixed prairie, and their significance has been confirmed by an increasing number of experimental exclosures, in all of which protection against grazing has enabled the mid-grasses to regain their normal dominance. In a few areas, especially on soils with the highest echard, overgrazing has led to the practical disappearance of the mid-grasses, but in none of these are the latter absent from protected spots in the vicinity.

Bunch-grass prairie of California. The valleys and hills of California are to-day covered with a continuous mantle composed of annual species of *Avena*, *Bromus* and *Festuca*. These have seemingly replaced the native perennials, *Stipa*, *Poa*, *Koeleria*, *Melica*, etc., so completely as to have produced grave doubt as to the composition of the original climax. In a country with winter rainfall, the perennial grasses are especially susceptible to damage by overgrazing during the annual dry period from May to December, and the outcome of 150 years of grazing and cropping has been to establish the wild oats as the one great dominant throughout. Because of its height and vigour it has been conserved for hay over large stretches and, since it also withstands grazing fairly well, it has come to simulate a climax in many respects. However, in recent decades, it has suffered more and more from overgrazing and is gradually being replaced by bromes, fescues and barleys.

The search for bunch-grass relicts in 1917–18 was first directed to trackways, not merely because such relicts were often remarkable in purity and extent, but also because they were rapidly being destroyed as a war-time measure to produce a great crop of wheat. Many hundred miles of a nearly continuous consociation of *Stipa pulchra* were obliterated in the Great Valley, leaving sparse fragments where plough and fire had taken lighter toll (Pl. IV, Phot. 8). It was especial good fortune to record these extensive relicts and then to have seen them reduced to patches here and there, as it not only confirms the other evidence to the effect that grassland was the original great climax of California, but it also throws needed light upon other regions known only by the mosaic of relicts.

The transformation of south-eastern California from bunch-grass prairie to desert as a consequence of climatic changes is attested by a variety of relicts in Death Valley, the Mohave, Colorado and Sonora deserts. For the most part these occur sparsely, a fact explained by the range of rainfall from 1 to 5 in., and are found chiefly on the mesoclines of the lower mountains and at altitudes of 3–5000 ft. in the higher ones. Sand and lava fields have formed a refuge for several of the most xeric species, while the most typical of all, the shrubby grass, *Hilaria rigida*, seems to have been derived directly from the adaptation of *H. jamesi* to a drying climate. Now a dominant of the south-western faciation of the mixed prairie, the earlier extension of the latter species over the desert region is proved by relicts in the mountain borders. This assumption as to the origin of *H. rigida* is further supported by its regular preference for sandy plains and washes with a higher water content.

True prairie. The key to the understanding of this climax association is to be sought in the place of origin and the life history of its dominants. Of the climax dominants, *Koeleria* and *Agropyrum* are circumpolar, while *Stipa spartea* is boreal, and *Bouteloua racemosa* south-western. *Andropogon scoparius* ranges well to both north and south, but it is southern in origin, while *Sporobolus asper* and *S. heterolepis* are essentially southern. The postclimax dominants of low prairie, *Andropogon furcatus* and *A. nutans* are widespread but of distinctly southern derivation, while *Panicum virgatum* is still more austral and *Elymus canadensis* northern. The preclimax Boutelouas and *Buchloë dactyloides* stretch to the Canadian border or beyond, but their original home is far to the south-west. The invading *Poa pratensis* is circumpolar, but the form in the true prairie has come from Europe by way of the East.

As a rule, the species of northern affiliation appear earliest in the spring and hence bear the heaviest brunt of grazing, as well as injury by spring fires. These are *Stipa spartea* and *Koeleria cristata* in particular; flowering occurs early likewise, in the central region during May. The preclimax short-grasses reach the optimum in early summer, *Bouteloua racemosa* in mid-season, and the postclimax tall-grasses in late summer, *Andropogon furcatus* and *A. nutans* blooming in late August or early September. *Sporobolus asper* is much the latest of all the dominants, the panicles often not appearing until the end of September. As the name June-grass indicates, *Poa pratensis* forms its flower culms early, at a time to give *Stipa* and *Koeleria* the keenest competition. *Agropyrum* blooms in midsummer, while *Andropogon scoparius* may slightly precede its taller relatives.

In terms of the competitive equipment of shoot and root, *Andropogon furcatus* takes first rank, followed closely by *Sporobolus asper*, and this by *Andropogon nutans* and *A. scoparius*. In spite of its tenacious rhizome, *Agropyrum* is a weak competitor, and the short-grasses maintain their place only by virtue of their xerocline proclivities. *Stipa* is fairly well equipped for holding its own, as is likewise *Bouteloua racemosa*, while *Koeleria* is rather less sturdy. However, the surprising competitor is the low and delicate *Poa*, but this owes its success in the chief degree to human coactions (Clements, Weaver and Hanson, 1929).

The basic relations of the dominants are clearly indicated in the three life forms, namely, tall-, mid- and short-grass, and are reflected in the harmony seen in the edaphic and climatic correspondences of each group. The tall-grasses occurred originally in the low prairie and still exhibit the best development there, as would be expected from their dominance in the subclimax prairie to the eastward. In other words, the tall-grasses are postclimax in the true prairie. The short-grasses are characteristic of ridges and xeroclines, in agreement with their climatic dominance in the more xeric mixed prairie to the west; they are in consequence preclimax. Finally, the seven mid-grasses occupy the general prairie levels between lowland and ridges, and constitute the actual climatic dominants. However, in the true prairie to-day, *Andropogon furcatus* is often found well up the slopes of rolling hills and sometimes on hill tops; *Stipa* and *Koeleria* are often much reduced or lacking, *Sporobolus asper* is usually entirely invisible in relict hay fields, and *Poa* has become widespread in swales and on cooler slopes especially.

The detailed explanation of these changes and the consequent reconstruction of the original prairie are too long for the present purpose, but the main features may be indicated briefly. The processes involved in the coactions of grazing, fire, mowing, clearing and settlement generally have exerted a selective action upon the various dominants in accordance with life form and life history. As the first forage in spring after stock have been on dry feed for several months, *Stipa* and *Koeleria* have suffered much more severely than any other dominants. Moreover, this places them at a disadvantage in their competition with *Poa* and handicaps them both in the persistence of the adults and the production of seed. Early burning is also a feature in some districts. At the other end of the growing season, the tardy *Sporobolus asper* is hampered by the practice of mowing in late August, so that storage in the crowns is reduced and the formation of seed prevented. Likewise it suffers more from fires set in the autumn, but in spite of these handicaps, its vigorous rhizomes keep its place as well as those of *Andropogon furcatus*, and its disappearance in relict hayfields is usually apparent rather than real. On the other hand, while the tall Andropogons are prized for hay, they are the least sought of the dominants by grazing animals. They thus possess a double advantage over *Stipa* and *Sporobolus*, and their spread up ravines and mesoclines is readily explained.

Fortunately, there is contemporaneous evidence of greater abundance previously for *Stipa* and *Koeleria* and of the upward march of the Andropogons in Kansas, Nebraska and South Dakota. Part of this is contained in herbaria and in lists and maps of distribution, supported in a general way by the widespread belief that the "bluestems followed the settler" (Bell, 1869). More important still is the printed record for Nebraska (Pound and Clements,

1898) and for South Dakota (Shepherd and Williams, 1894), as well as the journal of the Missouri and Niobrara grazing trip (Clements, 1893). In the forty years that have elapsed, the problem of changes in the true prairie has received continued attention, with the result that *Stipa*, for example, has been found in hundreds of relicts in Kansas, where it reaches its southern limit to-day. This is in spite of the fact that some observers say that they have never seen it in this state, presumably implying that it does not occur there.

Interpretation in scrub climaxes.

No other life form has raised so many difficulties of interpretation as the shrub. This is largely because of its size and visibility as contrasted with grasses, but partly also by reason of the ease with which it gives rise to savannah. At first thought, the latter conveys the impression of a climax, a view that needs to be corrected by careful consideration of the shrub as a climatic indicator, and especially by its peculiar relation to fire and browsing. While its life form indicates an intermediate position between tree and grass, this is true only in fairly humid regions; in arid ones, the typical shrubs are more xeric than grasses and hence become climax only in deserts. Another general misconception relates to the effect of fire, the perennial woody stems suggesting that scrub is injured more than grass by burning. This is true of a small number of shrubs, such as the sagebrush, *Artemisia tridentata*, which do not form root sprouts readily, but in the great majority of cases, fire increases the dominance of scrub at the expense of grass. When the latter is hampered by grazing, the disparity is even greater, and the effect of these combined coactions has everywhere been to develop scrub into a proclimax that masquerades as a true climax.

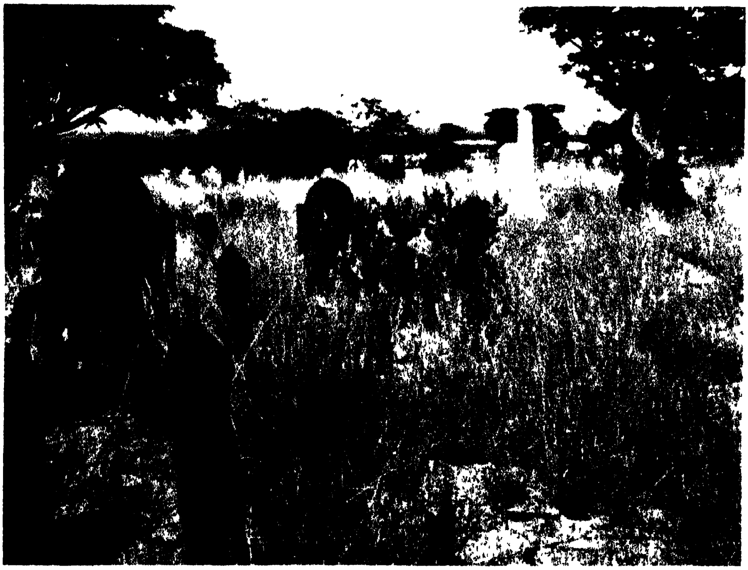
To permit this to happen, it is essential that shrubs be present upon which fire and grazing can operate. Such a situation was brought about by their northward migration in the wake of a climatic shift toward desert; in the south-west this might well have taken place at the time of the elevation of the Sierra Nevada during the Miocene. With the return of the grasses during an ensuing wet phase, the shrubs were enabled to hold their ground in favourable spots here and there, producing a very open savannah. It is probable that such stragglers increased slowly in number, especially during wet periods, but their great wave of abundance has undoubtedly been a consequence of man's coactions and chiefly during the historical period. This effect has been exerted upon three scrub communities of the south-west, namely, sagebrush, desert scrub and mesquite, all of which exhibit similar savannah relations in grassland. The differences between them are primarily an expression of life form and life history in relation to fire, grazing, and migration devices.

Sagebrush climax. The chief dominant, *Artemisia tridentata*, occurs as the most conspicuous plant over a vast extent of territory, and this has naturally led to regarding all this as climax. The search for relict grasses disclosed their presence throughout the major portion of the area, indicating that it is in reality sagebrush savannah. While sagebrush is browsed to a considerable degree, this is chiefly in the absence of a grass cover. Grass suffers much more severely under heavy pressure from stock, especially during drought periods, and has been rapidly replaced by *Artemisia* and its associates over most of the area concerned. This conclusion is in harmony with the record of changes in the vegetation of the Great Basin since the period of settlement, and is now placed beyond question by the evidence drawn from experimental exclosures.

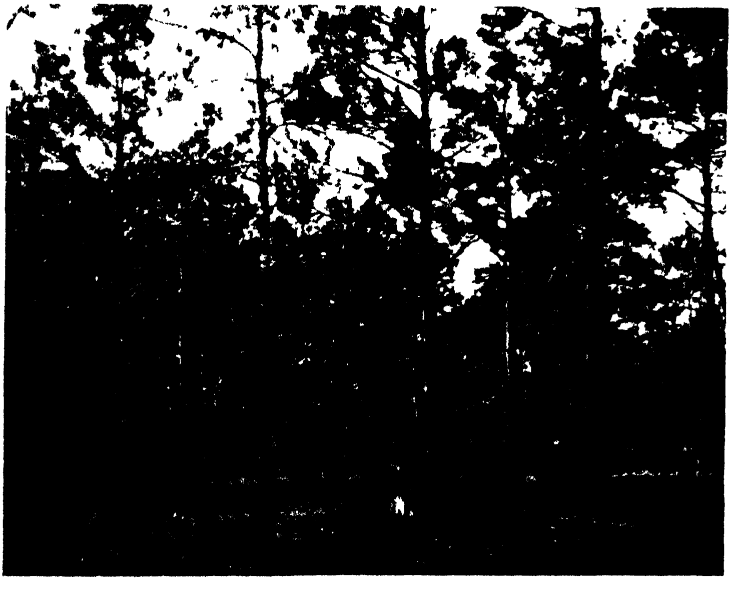
The region in which sagebrush constitutes a climax to-day is little more than a fourth of the area over which this species appears to be dominant. This is the driest portion, in which the grasses have disappeared under the swing toward desiccation, yielding their places to the more xeric bushes. The wide movement of the latter during the historical period has been almost wholly a consequence of overgrazing of the grasses. Fire has not been much utilised by stockmen, since it tends to reduce the browse, owing to the reluctance of the species to produce root sprouts.

Desert-scrub climax. A broad band of *Larrea tridentata* sweeps from western Texas through southern New Mexico and Arizona and adjacent Mexico into the desert regions of transmontane California and lower Nevada and Utah. Like the sagebrush, it is the most dominant note in the landscape, at the lower levels especially, and it is again understandable why it was mistaken for a climax community. Not only does it occupy a region early entered by man, but one also in which climate rendered grazing the major industry. In addition, it is a region in which drought is frequent and widespread, with consequent handicaps to grasses under the impact of grazing. This resulted in upsetting the climatic balance to the advantage of the shrubs, an effect enhanced by the necessity of yearlong grazing. As an outcome of the combined influence of climate and overgrazing, the control of the shrubs had come to appear complete, resulting in the designation of "arboreal desert."

For the reasons just given, the application of the relict method was attended with more than the usual difficulty. However, the existence of fine grasslands at elevations of 3000 ft. and higher, coupled with the amount and type of rainfall, made the assumption of a grassland climate and climax probable. The quest for relicts was a more arduous one, but attended with much the usual success, differing chiefly in the smaller number and size of the areas. Probably the most striking examples were those found in old cemeteries, the one at Tombstone, Arizona, affording a detailed record of composition and structure in a district where perennial grasses are practically absent (Pl. V, Phot. 9). Sand and gravel areas were also fruitful, while mountain mesoclines and canyons at low altitudes yielded all the species to be found as dominants in the existing desert plains at 3–4000 ft. Most illuminating of all were extensive areas of dominant *Bouteloua*, *Aristida* and *Sporobolus* during



Phot. 9. Desert-plains grassland, relict in the cemetery at Tombstone, Arizona.



Phot. 10. Fire subclimax of *Pinus taeda* in eastern Texas, with relict *Quercus* on the left.

CLEMENTS—RELICT METHOD IN DYNAMIC ECOLOGY

wet phases in the outskirts of Tucson, where hay had been cut within a generation. This was further corroborated by the presence of desert-plains grassland little modified under the protection afforded by Indian reservations, through the entire period of settlement. A unique and invaluable background to the discovery and interpretation of grassland relicts was the presence of the Santa Rita Range Reserve and the fenced grounds of the Desert Laboratory at Tucson.

By the combined use of relict grasses as indicators and of isohyets, it has been possible to draw a broad line between the *Larrea* savannah, which is in reality desert-plains climax, and the desert proper. The latter consists essentially of two dominants, *Larrea tridentata* and *Franseria dumosa*, with many less abundant or locally important associates. In general, the ecotone between them is outlined by the isohyets of 5 and 6 in. of rainfall. On the many broad outwash plains and the bajada slopes of the mountains are found postclimaxes of tall shrubs and small trees, among which *Carnegiea, Fouquiera* and *Yucca* are especially striking.

Mesquite postclimax. Throughout the *Larrea* savannah and the desert-scrub climax, *Prosopis* and *Acacia* are more or less typical of valleys and lowlands, constituting a fairly definite postclimax. Their water requirements explain why it is that in the higher rainfall of southern Texas they occupy the general level of the plain and give the appearance of a climax of low trees. In fact, the height and density of the individuals not infrequently justify such a conclusion, and a comprehensive analysis is required to disclose the real situation. Such a procedure was directed both to the behaviour of the individual and to the climatic and competition relations of scrub and prairie.

Though its associates resemble it in varying degree, *Prosopis* is unsurpassed in its success in migration and its powers of adaptation. Its sugary pods are eagerly sought by cattle, while the bony seeds are not affected by digestion and are voided under conditions especially favourable to successful germination. The leafy twigs are browsed to some extent, but the thorns prevent any serious damage from this source. Its powers of producing root sprouts are enormous and it is hardly possible for fire to be sufficiently frequent to kill it. Under the most adverse conditions it becomes decumbent in the form known as "running mesquite," in which it awaits the return of favourable circumstances. Its range of adjustment from such forms to trees of fair size give it a great advantage in competition with other woody plants and especially with grasses, so that it is regularly the chief dominant in the postclimax.

From the preceding, it becomes clear that the current assumption that fire favours grassland at the expense of mesquite is incorrect. In short, all the evidence demonstrates that instead of mesquite being eliminated by prairie fires, it has been decisively favoured by them. Although the native grasses are not injured by fire as a rule, they derive no such advantage in competition as that secured by *Prosopis* from the increased number of shoots and density of individuals, particularly when dissemination by cattle is taken into account. As to the food coaction, mesquite is usually damaged little or not at all by browsing, while overgrazing may remove the grasses more or less completely, again giving the mesquite a decisive advantage in the competition. Taken in combination, these features readily explain the great extent of mesquite and its ability to simulate the rôle of a climax dominant.

The repeated examination of the mesquite postclimax over a large part of its range discloses the general presence of grass relicts, except where grazing has been most severe, resulting in the production of "motts" or grooves with a fairly close canopy. The usual condition is that of a more or less open savannah, in which the composition and density of the grass cover vary with the degree of grazing. In the absence of overgrazing and frequent burning, the grassland is more or less typical coastal prairie with mesquite dotted over it.

Chaparral climax. Chaparral differs essentially from the communities just considered in being truly intermediate between forest and grassland. It resembles them inasmuch as the majority of the dominants form root sprouts readily when cut or burned; as a rule they are browsed but little and none of them exhibit the ready migration of mesquite. As a climax, chaparral is at its optimum in California, where it is typically evergreen; toward the east it gradually loses this character, as well as much of its massiveness.

The interpretation of chaparral has been chiefly concerned with the question of its climax nature and its relation to grassland, especially as to their relative extent in former times. The first could be solved only by an intimate analysis of the zone of scrub lying between the grassland and the montane forest. At the lower edge where it forms savannah with the bunch-grass prairie, the dominants proved to be different as to genus and life form. It was soon realised that their affinities were with the sagebrush rather than chaparral and that they constituted a coastal association of the former, now chiefly represented by savannah. In the lower portion of the montane climax, the life form and genera were those of the chaparral proper, but the species mostly different, constituting a fire subclimax destined to yield to coniferous forest. Between these two zones lies the mass of the climax chaparral, subject to recurring fires and regenerating rapidly and universally by means of root sprouts.

In the absence of the zone of coastal sagebrush, chaparral often lies in contact with bunch-grass prairie and then forms a belt of savannah of varying width. This is chiefly true of its major dominant, *Adenostoma fasciculatum*, which is the most xeric constituent and hence occupies the lowermost position as a rule. Like most savannah shrubs, it maintains itself best in broken or rocky ground against the competition of grasses and in such places forms small postclimax groups. During wet phases of major climatic cycles, *Adenostoma* and chaparral generally doubtless extended further down mountain-side and foothill, but the present relations have probably obtained since the last great pulsation of the Pleistocene.

The gradual encroachment of the grasses and a small amount of clearing have slightly diminished the area of chaparral during the historical period in California, but these processes have operated chiefly upon the coastal sagebrush. The field work of the past fifteen years has placed beyond question the conclusion that the spatial relations of grassland and chaparral have long been essentially what they are at present. The recording of many thousand grass relicts wherever the various types of protection exist renders it certain that the Sacramento and San Joaquin valleys, the many intermountain valleys, and the hills and lower ranges have belonged to the grassland climax for millennia past. This is supported by the universal absence of chaparral relicts in these regions and by historical records of the days of exploration, and finally confirmed by the course of competition between grass and scrub under protection.

Interpretation in forest climaxes.

The most important and fascinating questions in the interpretation of forest communities pertain to the nature and movement of climaxes. Because of the large number of forest climaxes and their location in regions of general or local glaciation, the problem is more complex than with either scrub or grassland, and it is further diversified by the long ecotones that these make with forest. Hence, it has been necessary to approach it from three different directions, namely: (1) reciprocal relicts within or between forest climaxes; (2) relicts in the ecotone between forest and grassland or scrub, and (3) those resulting from human coactions, chiefly fire or lumbering. However, in all of these the outcome follows the rule that life form and life history are the decisive features. Trees, like shrubs, are browsed, but this affects only the lower branches and has no significance except for seedlings or sprouts. Among trees themselves, the most striking difference is in response to fire, broad-leaved species as a rule sprouting readily, while this function is regularly absent in conifers, redwood being the most notable exception. Furthermore, some conifers are highly resistant to ordinary fires, as exemplified by *Pinus ponderosa* and *P. palustris* in particular. A few relicts are produced by fungus and insect coactions; the outstanding instance is that of *Castanea* and *Endothia*, the chestnut being completely killed over wide areas or so badly damaged as to persist only in the form of root sprouts.

Deciduous forest climax. Probably no other formation on the continent contains such a host of relicts in the form of preclimaxes and postclimaxes. This is due in part to the large number of dominants and the long ecotones between the three associations, arising from the fact that the maple-beech and chestnut-oak are enclosed on three sides by the oak-hickory community. More significant still is the marked dissection of the Appalachians and their flanking plateaux, such as the Cumberland and Allegheny, over which the various climaxes have moved in phalanx under the compulsion of glacial and interglacial climates. The mosaic of relicts has been further varied by the pathway afforded for the southward migration of the pine-hemlock and the spruce-balsam climaxes along the crest of the ranges.

As a consequence, the relatively xeric oak-hickory community appears as preclimaxes on xerocline slopes and ridges through much of the maple-beech and the chestnut-oak associations. Conversely, these more mesic communities constitute postclimaxes on mesoclines and in coves and valleys of the oak-hickory climax. Such intercalations or enclaves are especially numerous along the line of ecotones, but they frequently extend far into the mass of each association likewise, as exemplified by postclimax relicts of beech near the Gulf of Mexico. This wide distribution is probably to be explained by the greater compensatory effect of topography in the case of a climax flourishing within a rainfall of 40–60 in., by contrast with a range from 40–6 in. in the grassland climax.

The existence of relicts of white pine and hemlock in the maple-beech and chestnut-oak climaxes especially likewise reflects the compensating action of topography, though this includes temperature as well as water relations. Near their southern limit, postclimaxes of hemlock in particular require the protection afforded by both mesoclines and canyon-like valleys. Such relicts have usually been regarded as an intrinsic part of the surrounding deciduous climax, but this is a reflection of the static viewpoint. Not only is this view discounted by the life form, but it is also emphatically contradicted by the regular association of the hemlock and white pine in their climax region about the Great Lakes. Recently, this conclusion has been reinforced by the studies of hemlock relicts in Indiana by Friesner and Potzger (1932).

As the region of earliest and densest settlement by Europeans, the deciduous forest has borne the brunt of human coactions in terms of fire, clearing and lumbering. These have wrought profound changes in the climaxes, often of such wide extent as to cause their reference to climatic or edaphic factors. The true explanation of the pine forests of the south-east especially was first suggested by the detailed study of burn successions characterised by closed-cone pines in other parts of the country, notably *Pinus contorta* in Colorado (Clements, 1910) and *P. divaricata* in Minnesota (Bergman and Stallard, 1916; Stallard, 1929). Repeated reconnaissances through the coastal plain from New Jersey to Texas confirmed the similarity of these subseres, and at the same time revealed the constant presence of relicts of the original climax of deciduous trees (Pl. V, Phot. 10). In his studies of climax and sere in North Carolina, Wells (1924, 1928) had reached the same conclusion as to the climax, and this view was further supported by the work of Tharp in eastern Texas (1926). In addition to oak-hickory relicts in all degrees of mixture with pines, there are frequent relicts of beech and other species postclimax to the oak-hickory in this region.

A recent analysis of the several burn consocies from New Jersey to southern

Florida and west to Texas has left no doubt that this region belongs to the oak-hickory climax and that the abundant hardwood relicts would again take possession under proper protection, especially from fire (Clements, 1932). This journey was made during a drought period in which fire was almost universal, and the paramount significance of this process was much more convincing than it could have been at any other time. Explicit testimony to the paramount rôle of fire was also discovered in the so-called "plains" of New Jersey, which are barrens clothed with a dwarfed spreading life form a few feet tall. To the student of succession, this was obviously an effect of fire, a conclusion confirmed by finding the same adaptation in a recent burn surrounded by tall pines and relict oaks. The universal rôle of fire in the south-east was further attested by the grass and heath balds of the Great Smoky Mountains. Various causes have been advanced in explanation of these, but the constant and especially the recent evidences of fire place beyond question the fact that they represent subclimaxes in the burn subsere (Clements, 1932).

Frequent reference has been made to the relicts of the oak-hickory climax that front the prairie or still linger in it. These are the most conspicuous and in some respects the most eloquent of relict communities, chiefly because of the differences in the life forms and climatic relations of the respective dominants. In the widespread shrinkage of the deciduous forest before advancing desiccation, advantage was taken of every compensating feature, and this serves to explain the numerous fringing forests of streams from Saskatchewan to Texas, the unique relicts in deep cool canyons, and the climax-like savannahs of mountain outliers and sandy plains in Oklahoma and Texas.

The most dramatic event of the period of desiccation was the falling back of the forest along the line of the isohyet of 40 in., running from central Missouri through southern Illinois and into Indiana. The spearhead of the prairie advance reached Ohio and southern Michigan, where a few relict areas still persist. From here westward to the Mississippi the hold exerted by the grasses through competition has delayed the return of forest, and through the period of settlement fire and clearing have co-operated to make this slower and in many places impossible. In consequence, this great wedge of subclimax prairie will long be represented by relict areas within the climate of forest—perhaps indeed until both forest and prairie have practically vanished before cultivation.

Coniferous climaxes. On the west, the contact between prairie and forest is regularly constituted by conifers. The most extensive ecotone is that between mixed prairie and woodland consisting of juniper and pinyon (*Pinus edulis*). Like the oak-hickory forest, this has undergone extensive shrinkage as a result of desiccation, and over three-fourths of its area exists only in the form of savannah in a grassland climate. Relicts of the actual climax still persist at higher elevations in sufficient number and mass to serve as a basis for tracing the process of shrinkage and the concomitant invasion by the grassland.

In the task of interpretation, however, it has been necessary to reckon with two facts of importance. The one is the ability of the woodland dominants to invade talus slopes earlier than the grasses, only to be replaced by the latter, and the other the facility with which juniper increases in density and extent as a consequence of dissemination by birds, sheep, and goats into areas where the occupation of grasses is much weakened by overgrazing. In California, the annual dry season has emphasised the effects of desiccation, and the woodland exists to-day only in savannah form or isolated fragments, in which the Joshua tree (*Yucca brevifolia*) is sometimes a unique dominant.

Along the central mountain ranges, the woodland is absent and the advancing grassland has taken the places left by the vanishing pines (*Pinus ponderosa* and its varieties). The process of shrinkage is similar in all essentials to that for woodland, and the outcome is likewise the production of a broad belt of savannah. On the east, three great relicts still persist, two of them in the form of plateau savannah on Cheyenne Ridge and Pine Ridge in western Nebraska. The other occurs as pine climax in the Black Hills of South Dakota, where it is associated with relicts from the boreal climax, namely, *Picea canadensis*, *Betula alba papyrifera* and *Populus tremuloides*. In California, the withdrawal of the yellow pine has apparently led to the evolution from it of a relict species (*Pinus torreyana*), now surviving only around the Soledad Estuary at La Jolla and on Santa Rosa Island near Santa Barbara.

A similar evolution of new species from the dominants of shrinking climaxes has been a remarkable feature of climatic changes in California. Apart from the universally known *Sequoia gigantea* and *sempervirens*, these comprise five pines, viz. *Pinus radiata* and its variety *binata*, *muricata*, *attenuata*, *sabiniana* and *coulteri*, five cypresses, *Cupressus macrocarpa*, *goveniana*, *guadalupensis*, *macnabiana* and *sargenti*, *Pseudotsuga macrocarpa* and *Abies venusta*. The position of all of these in terms of latitude and altitude would indicate that they have developed under more xeric conditions than those in which their probable ancestors dwelt and that a continued shift toward desiccation has resulted in isolation and shrinkage, which have nearly led to extinction in the case of *Pinus torreyana*, *P. radiata* and the species of *Cupressus*. It is not improbable that several other species of restricted area on the Pacific Coast have passed through a similar history, for example, *Pinus lambertiana*, *P. jeffreyi*, *Picea breweriana*, *Abies magnifica* and *Chamaecyparis lawsoniana*. In this connection, it is interesting and possibly significant that the south-eastern United States exhibits a group of several endemic species of pine, and the southern Appalachians the apparently relict *Tsuga caroliniana* and *Abies fraseri*. In all of the species mentioned, evolution and restriction are most plausibly related to the southward migration of the ancestral stock or to later shrinkage under a warmer or drier phase of a major cycle.

NATURAL AREAS AND RESEARCH RESERVES.

While national forests and grazing reserves have afforded opportunity for much ecological investigation, this has necessarily been focused in large degree upon regulated utilisation. With the rapid accession of interest in natural and wilderness areas and in research reserves, a new vista is opened to scientific research in national and state parks, national forests and similar preserves. To realise this adequately, the methods of dynamic quantitative ecology are indispensable, and a comprehensive system has been developed for this purpose. This rests upon the biome as the basic unit and upon climax and succession as the two paramount objectives. It employs the relict method as the key to both the past and the future, and places proper emphasis upon the measurement and record of community functions and changes by means of quadrats and exclosures.

The essential features of such an ecological system are: (1) reconnaissance of the area, (2) selection of particular communities or portions, (3) detailed survey, (4) installations for exclosure and experiment, (5) records in the form of maps, notes, charts and photographs to serve as standards, for (6) valuation study and re-survey at intervals of five to ten years. Perhaps the greatest lack of dynamic ecology has been the continuous tracing of succession and other changes, because of the length of time involved, the absence of control over desirable communities, and the difficulty of securing long-term co-operation. With the establishment of research reserves of various types, the first two handicaps disappear and the solution of the third becomes the sole problem, which demands immediate attention. This is now being given in America and it is noteworthy that a beginning in this respect has been made in the Antipodes at Arthur's Pass, a national forest of New Zealand (Cockayne and Calder, 1932).

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THE PHYSIOLOGY OF XEROPHYTISM IN AUSTRALIAN PLANTS

THE STOMATAL FREQUENCIES, TRANSPIRATION AND OSMOTIC PRESSURES OF SCLEROPHYLL AND TOMENTOSE-SUCCULENT LEAVED PLANTS

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INTRODUCTION.

THE structural changes found in the foliar organs or modified foliar organs of xerophytic plants were regarded according to the classic view as modifications of an archetypical mesophytic leaf. In all cases it was considered that these modifications reduced the amount of transpiration in the xerophytic plants (**7**, **25**, **26**, **29**). Modern work has suggested that this idea of xerophytes has been a generalisation on insufficient data. Maximov and his collaborators (**2**, **15**) have shown that succulent plants have a low intensity of transpiration, but that hard-leaved xerophytes and xerophytes with semi-succulent leaves transpired more than mesophytic leaves under high tension of meteorological factors. They showed also that the yield of xerophytes like *Artemisia fasciculata* and *Zygophyllum fabago* was increased if the water content of the soil were increased. Our own experiments with *Atriplex vesicarium* and *Kochia sedifolia*, typical plants of the Shrub Steppe, show a similar result.

Maximov considers plants such as these to be drought resistant rather than plants to which dry conditions are actually beneficial; he considers a capacity to endure permanent wilting as the basis of actual drought resistance. This is bound up in some way with changes in cell colloids, but the mechanism he leaves obscure. He divided "xerophytes" into two types, succulents and "true xerophytes," and considered the former to be not typical but highly specialised and relatively restricted forms.

Stocker (**27**) concluded from his work on desert plants that the gradation of transpiration values in these plants was of the same order as that found in plants from other habitats. He emphasised the fact that there is no single xeromorphic type, but recognised provisionally four types: succulents, herbaceous-leaved types, grass-leaved types and ericoid-leaved types.

MacDougal and Spalding (**14**) divided desert plants into two groups; plants with indurated leaves and succulents. The latter they considered to constitute a more specialised condition of xerophytism.

Wood (**31**) grouped arid plants into three groups: stem succulents, indurated microphylls and tomentose-succulent microphylls.

Modern work, especially that of Yapp (**37**) and Zalenski (**38**), has considered the essential anatomical features of xerophytes to be a decrease in the size of all cells, including stomata; a thickening of cell walls; strong development of palisade mesophyll; a denser network of veins, and an increase in the number of stomata per unit area. Physiologically there is an increase in the intensity of transpiration, an increase in osmotic pressure and in the capacity to endure permanent wilting.

COMPARISON OF THE SCLEROPHYLL LEAF TYPE AND THE SEMI-SUCCULENT LEAF TYPE.

The concept of the mesophytic type does not enter largely into the experience of the Australian botanist. The sclerophyll type of leaf in both tree and shrub is dominant in all the vegetation communities in the areas with heavier rainfall (12–45 in. per annum). The sclerophyll leaf agrees in many particulars with the criteria summarised by Maximov (**15**) for the essential anatomical features of xerophytes. It will be shown that it is doubtful if these criteria are of greater value in defining a xerophyte than the older ones of sunken stomata, heavy cutinisation and so on.

The commonly accepted definition of a sclerophyll plant community is an association developed under conditions of fairly high winter rainfall and summer drought. But in Australia, whilst sclerophyll formations typical of this Mediterranean type of climate are found in greatest abundance in the south-west of Australia and in the Mount Lofty Ranges of South Australia, they are also found in Victoria with a practically uniform rainfall, along the eastern coast of New South Wales and extending into Queensland. In the latter regions the rainfall is 40 in. per annum or more, with a summer maximum, and with at least 2 in. of rain during each month. Here also the annual rainfall greatly exceeds the annual evaporation.

At the other extreme, communities of sclerophyll plants are characteristic of the mallee, brigalow and the desert scrub. In South Australia with its winter rainfall mallee is found between the 20 and 8 in. isohyets (**34**); while in north-eastern Australia within the same limits, but with a summer maximum, brigalow (a semi-tropical thorn scrub dominated by *Acacia harpophylla*) alternates with savannah. Within the 8 in. isohyet two co-climatic plant associations are developed: Desert Scrub (**19**) found on rocky hills and on sandhills where water is more conserved, and Shrub Steppe found on the more arid plains. The Desert Scrub consists of sclerophyll plants, but the Shrub Steppe of semi-succulent chenopodiaceous plants.

In all climates in Australia, except that which permits of rain forest development and is dominated by plants of Malayan origin, the trees and the perennial vegetation generally are all of the sclerophyll type.

The essential features of the sclerophyll leaf, *i.e.* thick-walled and often lignified cells, Maximov, following Yapp (**37**), ascribes to intense solar radiation and a water deficit in the leaves which leads to a deflection of water from the embryonic tissues. This shortage of water does not permit normal development of the cells during the period of cell enlargement so that the cell walls soon cease to expand and become thicker. Maximov considers that decrease in cell size leads to other structural changes.

The problem of xerophytism must be viewed on a broader basis than that of water relations alone. Insolation in Australia is intense, and if assimilation is more active it is conceivable that much carbohydrate may be converted into cell wall material. It has been shown, however, that in desert plants (**36**) the rate of assimilation is considerably lower than in mesophytic plants (**13**). Further, carbohydrate metabolism follows two courses in arid plants—one leading to pentosan formation and the other to the formation of uronic acid complexes and of lignin (**36**).

In the more humid regions in eastern Australia where sclerophyll plants occur, it is not conceivable that water deficits in the leaves should be important as a determining factor.

Apart from the above-mentioned factors it is probable that mineral nutrients may play a part in the determination of the sclerophyll habit. The greatest aggregations of individuals and of species in sclerophyll communities are found on the sand plains in South Australia and also in the arid regions. These plains are deficient in mineral bases other than alumina and iron and the vegetation consists of a dense assemblage of low shrubs and undershrubs with ericoid or needle-like leaves. Even in the savannah forests, wherever ironstone develops, the grass-like undergrowth is replaced by a dense growth of spiny sclerophyllous shrubs.

In South Australia the sclerophyll forests have been studied in some detail (**1**, **35**) and the leaf types fall into two groups—the broad sclerophyll and the ericoid. In the arid areas within the 8 in. annual isohyet the sclerophyll leaf is characteristic of the Desert Scrub. Here the needle-like leaf or phyllode predominates and species of *Acacia*, *Cassia*, *Eremophila* and *Dodonaea* form the bulk of the scrub.

The composition of the Shrub Steppe varies with the soil type. Pure shrublands of *Atriplex vesicarium* occur where there are 1 or 2 in. of sandy loam over a more or less solid layer of limestone in the B horizon. Where the limestone reaches the surface *Kochia sedifolia* is locally dominant. On the more mature plains with 9–12 in. of loam over the limestone *Atriplex vesicarium* and *Kochia planifolia* are co-dominant while other chenopodiaceous plants, especially species of *Kochia*, *Bassia* and *Rhagodia* are sub-dominant. These plants are the only permanent members of the formation although a wealth of ephemeral plants, chiefly composites and crucifers, are found after rains.

The leaf type of the plants of the Shrub Steppe is entirely different from the sclerophyll types so far considered. It is semi-succulent, but in practically all cases the leaves are covered with dense masses of epidermal hairs or the more humid habitat. Compared with the trees and shrubs of the British woodlands the difference of means and the standard error of difference is 108 ± 23 for the wet patanas and 89 ± 29 for the dry. The differences in stomatal frequency as shown from these sets of data must be regarded as significant. In view of the variation in stomatal frequency from leaf to leaf on the same plant, and in different portions of the same leaf, it is difficult to assess accurately the value of the Ceylon figures.

In the investigations on Australian plants leaves were taken from plants in diverse stations, usually from five different plants, and counts were made on leaves near the ground, about half-way up the stem and from the top of the plant. Usually ten determinations were made on each leaf, so that for statistical purposes it is probable that the average figure for the stomatal frequency is one which can be relied on, and can be used for comparison with those obtained by Salisbury.

In Table II are given the mean stomatal frequencies of trees and shrubs from the sclerophyll forests of the Mount Lofty Ranges. This formation is developed in areas with an average annual rainfall of from 25 to 40 in.; 70 per cent. of the rain falls in the winter months and the remaining months are very dry.

Table II. *Stomatal frequencies of plants from the sclerophyll forests of South Australia.*

	Upper surface	Lower surface	Total
Family Proteaceae			
Hakea rugosa	70	70	140
H. ulicina	93	93	186
H. rostrata	49	49	98
H. gibbosa	70	70	140
Isopogon ceratophyllus	102	102	204
Conospermum patens	117	112	229
Adenanthos terminalis	49	49	98
Persoonia juniperina	30	32	62
		Average	145 ±19·0
Family Loranthaceae			
Loranthus pendulus	140	140	280
Family Pittosporaceae			
Billardiera scandens	124	0	124
Cheiranthera linearis	90	0	90
Family Leguminosae			
Pultenaea daphnoides	0	212	212
P. floribunda	200	0	200
P. largiflorens	195	53	248
Platylobium obtusangulum	0	294	294
Acacia pycnantha	146	146	292
A. obliqua	185	185	370
A. rupicola	120	115	235
A. juniperina	192	192	384
A. linearis	183	183	366
A. longifolia	155	155	310
A. myrtifolia	58	58	116
A. rhetinoides	148	148	296
		Average	277 ±21·7

Table II (*contd.*).

	Upper surface	Lower surface	Total
Family Myrtaceae			
Leptospermum scoparium	136	138	274
Eucalyptus leucoxylon	135	135	270
E. fasciculosa	220	220	440
E. odorata	192	192	384
E. Baxteri	112	112	224
E. obliqua	151	90	241
		Average	307 ± 32
Family Tremandraceae			
Tetratheca ericifolia	0	255	255
Family Epacridaceae			
Astroloma conostephioides	0	300	300
A. humifusa	0	290	290
Acrotriche serrulata	0	320	320
A. fasciculiflora	0	300	300
Leucopogon virgatum	0	317	317
Epacris impressa	0	285	285
		Average	302 ± 5
Family Compositae			
Ixodea achilleoides	56	84	140
Family Liliaceae			
Xanthorrhoea semiplana	133	133	266
Family Cyperaceae			
Lepidosperma viscosum	288	288	576

The mean stomatal frequency of these thirty-nine species which are the characteristic plants in the sclerophyll forests is 230 ± 19. Comparing this figure with that of the trees and shrubs of the British woodlands, one finds that the difference of means and the standard error of difference is 19 ± 23, so that there is no significant difference in the number of stomata in plants from the two habitats. Further, if the plants from the sclerophyll forest are divided into undershrubs (less than 1 m. high), and tall shrubs and trees (over 1 m. high), the stomatal frequencies are 252 ± 22·8 and 248 ± 20·8 respectively. There is, therefore, no significant difference in stomatal frequency between the plants of the two strata. This result is at variance with Salisbury's findings for British woodlands.

The leaves of plants in the sclerophyll forests can be divided into three classes: the *broad sclerophyll* with a mean stomatal frequency of 287, the *ericoid* with a mean frequency of 279, and the *needle-leaved* plants with a mean frequency of 101. It will be seen that the difference in stomatal frequency between the ericoid and broad sclerophyll types is not significant, but that there is a marked difference in the needle-leaved type when compared with the others.

The majority of the plants comprising the sclerophyll communities fall into a few well-marked families as may be seen from Table II. It is evident that family and more especially generic characters play a large part in determining stomatal frequency, and for this reason the needle-leaved plants, which belong mainly to the Proteaceae, have a low stomatal frequency. The mean frequencies of the chief families in the sclerophyll forests are shown in Table III.

Table III.

Family	Stomatal frequency
Proteaceae	145 ± 19·0
Leguminosae	277 ± 21·7
Myrtaceae	307 ± 32·0
Epacridaceae	302 ± 5·0

The stomatal frequency in the Proteaceae, while showing a range, is consistently low. The Epacridaceae which plays an important part in the lower strata is a well-defined family with a very constant stomatal frequency as shown by the small standard error. This family is the only one of importance in the sclerophyll communities in which the stomata are confined to the lower surface. Within the Leguminosae, the genus *Pultenaea* shows wide variation in the three species examined, stomata being confined to the upper or lower surface or found on both surfaces. This is a plastic genus with many varietal forms. The large genus *Acacia* also shows variation but the frequency is consistently high. In the Myrtaceae, and especially in the plastic genus *Eucalyptus*, variations also occur.

Further evidence for the tendency of certain genera to maintain a constant stomatal frequency is found in plants of the arid communities, especially in the genera *Kochia* and *Bassia* of the Chenopodiaceae and in *Eremophila* of the Myoporaceae. (See Table IV.)

Generally speaking, it appears evident that family or generic characters play a part in determining the mean stomatal frequency of any community of plants quite apart from any environmental factors which may be operative.

Wilson (**30**) has listed the stomatal frequencies of a number of plants from different habitats in Victoria. These plants were grown in pots and used for transpiration experiments. Considering only the sclerophyll plants, we have calculated the mean frequency and its standard error from his data. This is 190 ± 15, which shows no significant variation from the mean frequency calculated for the plants from the Mount Lofty Ranges.

The plants from the arid areas that have been examined were collected in the neighbourhood of the Koonamore Vegetation Reserve. This area has an average annual rainfall of 8·12 in., and rain falls on the average about 30 days per annum. As pointed out previously (**18**), only about one-third of this rainfall is effective as far as the roots are concerned; the remainder, falling in small amounts during the dry periods, does not penetrate the surface mulch of the soil.

In this area two co-climatic associations occur—the Desert Scrub and the Shrub Steppe—the latter being characteristic of a more arid environment than the former (**4**, **16**, **17**, **19**). Stomatal frequencies of plants from both these communities are shown in Table IV.

Table IV. *Stomatal frequencies of plants from the arid communities of South Australia.*

	Upper surface	Lower surface	Total
Family Proteaceae			
Hakea leucoptera	53	53	106
Family Chenopodiaceae			
Bassia biflora	32	32	64
B. uniflora	48	48	96
B. limbata	52	52	104
B. obliquicuspis	31	31	62
B. patenticuspis	23	23	46
B. paradoxa	28	28	56
B. sclerolaenoides	25	25	50
Kochia sedifolia	50	50	100
K. Georgii	24	24	48
K. tomentosa	36	36	72
K. triptera	14	14	28
Atriplex vesicarium	120	120	240
A. stipitatum	128	128	256
Rhagodia Gaudichaudiana	114	114	228
R. spinescens var. deltaphylla	110	110	220
Salsola Kali	56	56	112
		Mean	115 ± 18·7
Family Amarantaceae			
Trichinium obovatum	37	37	74
Family Sapindaceae			
Heterodendron oleifolium	55	55	110
Family Leguminosae			
Acacia aneura	112	112	224
A. Burkittii	112	112	224
Cassia Sturtii	110	110	220
Family Myoporaceae			
Myoporum platycarpum	130	105	235
Eremophila Brownii	92	103	195
E. Duttonii	70	94	164
E. maculata	115	118	233
E. Sturtii	119	78	197
E. longifolia	128	121	249
		Mean	212 ± 12·0

All the plants in the above list belong to the Desert Scrub, with the exception of the Chenopodiaceae which are members of the Shrub Steppe.

The mean stomatal frequency of the sclerophyll plants is 197 ± 14. The mean frequency for the plants of the plains is 115 ± 18·7. Considering the sclerophyll plants first, and comparing them with the British woodland plants, one finds that the difference of means and the standard error of difference is 14 ± 20. This indicates that there is no significant difference in the mean number of stomata for the two groups. Compared with the sclerophyll plants of the Mount Lofty Ranges the difference of means and the error of difference is 40 ± 23, showing again no significant difference in stomatal frequency. Comparing the desert sclerophylls with the plants of the dry patanas, the difference of means is 103 ± 30, showing a significant difference in frequency. It has been pointed out before that complete reliance cannot be placed on the results of Parkin and Pearson since at the time of their determination the extreme variability in stomatal frequency in one plant was not realised. It cannot therefore be said with certainty that the plants of the more tropical and humid climates have a higher stomatal frequency than plants from arid areas, although this has been the commonly accepted view. The fact that the stomatal frequencies of plants from both the wet and the dry patanas show no significant difference in spite of the different climates points to the conclusion that stomatal frequencies are not influenced to a great extent by environmental conditions.

Summing up the results as regards trees and shrubs, it may be said that the mean stomatal frequency of any community of sclerophyll plants from desert or from moister regions does not show greater variation than do plants of non-sclerophyll moist habitats. This result agrees with Stocker's observations that the transpiration values of desert plants show the same order of gradation as those from other habitats. The available counts of mean stomatal frequency in plants from various communities are listed in Table V.

Table V. *Mean stomatal frequencies for trees and shrubs.*

Habitat	Author	Mean stomatal frequency
British woodlands	Salisbury	211 ± 14·2
Wet patanas	Parkin and Pearson	319 ± 21·0
Dry patanas	Parkin and Pearson	300 ± 26·0
Sclerophyll forests, South Australia	Wood	237 ± 19·0
Sclerophyll forests, Victoria	Wilson	190 ± 15·0
Desert Scrub	Wood	197 ± 14·0
Shrub Steppe	Wood	115 ± 18·7

There remains for consideration the group of perennial plants found on the arid Shrub Steppe, which with one or two exceptions belong to the Chenopodiaceae. The mean stomatal frequency of these plants is 115 ± 18·7; a low figure showing a significant decrease when compared with plants from any other habitat that has been examined. It has been pointed out that these plants can be divided into two groups as regards leaf form. These two types show marked differences in mean stomatal frequency; the mean of the flat type is 249 ± 8·1, a number which shows no significant variation from that of the sclerophyll plants. On the other hand the cylindrical leaves of the genera *Bassia* and *Kochia* show a much lower mean frequency, namely 79 ± 7·4. These figures again indicate the importance of generic characters in determining the mean stomatal frequency.

The plants of the Shrub Steppe are peculiar not only in their water absorption but also in possessing a low stomatal frequency.

POSITION OF THE STOMATA.

The position of the stomata on the upper or lower surface of the leaves varies considerably, apparently in relation to environmental conditions. In this case also it appears that family or generic characteristics may determine stomatal position, as in the family Epacridaceae in which stomata were confined to the lower surfaces in all species which have been examined.

The factors determining the presence or absence of stomata in relation to surface are not clearly understood. Salisbury (**24**) found that in general the upper surfaces of leaves of trees and shrubs in British woodlands were devoid of stomata, but that more than one-half of the ground flora developed stomata on the upper surface. The fact that of 106 species of mat-like plants from the Alps all had stomata on the upper surface led Lohr (**12**) to conclude that the greater degree of exposure caused development of stomata on this surface.

Table VI shows the proportion of stomata on both surfaces of the leaves in plants from different habitats.

Table VI. *Showing percentage of plants with stomata present on both surfaces of the leaves.*

Habitat	%
British woodlands	5·4
Dry patanas, Ceylon	35·0
Wet patanas, Ceylon	41·0
Sclerophyll forest, South Australia	79·0
Sclerophyll forest, Victoria	88·0
Arid communities, Koonamore	100·0

It is evident that the high percentage of plants possessing stomata on both surfaces in the case of the sclerophyll and other plants of arid habitats possesses a real meaning and is possibly correlated with increasing aridity.

STOMATAL SIZE AND STOMATAL INDEX.

In spite of variations in stomatal frequency found in different plants of the sclerophyll group, the pore area per sq. mm. tends to a constant value. The mean pore area of the stomata at their maximum opening was measured in living plants from camera lucida outlines, the area of the enlarged pore being measured with a planimeter. The pore area per sq. mm. is the mean area of the pore multiplied by the mean number of stomata per sq. mm. Leaves with extremes of stomatal frequency were chosen, and the results are shown in Table VII.

Table VII.

Species	No. of stomata per sq. mm. on one surface	Mean area of pore in sq. mm.	Pore area per sq. mm.
Persoonia juniperina	30	0·000754	0·0466
Eucalyptus Baxteri	112	0·000204	0·0457
Eucalyptus fasciculosa	220	0·000099	0·0446

The pore area per sq. mm. is approximately constant. It would be expected from the laws of multi-perforate diffusion that the transpiration would be greater in leaves in which the stomata are closer together, since evaporation is proportional to the diameters and not to the areas of the stomata.

The stomatal indices (**24**), as far as these have been investigated, tend to be constant. The values approximate to the mean value given by Salisbury for British woodland plants. These values are given in Table VIII.

Table VIII.

Species	No. of stomata per sq. mm.	No. of epidermal cells per sq. mm.	Stomatal index
Persoonia juniperina	30	135	18·1
Platylobium obtusangulum	294	1253	19·0
Pultenaea daphnoides	212	1121	18·0
Eucalyptus Baxteri	224	900	19·9

TRANSPIRATION.

It has been shown in the previous sections that the mean stomatal frequency of any group of plants, except that of the Shrub Steppe, tends towards a constant value. It might be expected therefore that, given similar conditions, the mean transpiration of any group should also be constant. In sclerophyll plants cuticular transpiration is reduced to a minimum, so that stomatal control might be expected to play a considerable part in determining transpiration.

It is difficult to compare the results of different observers owing to varying environmental conditions. The relative transpiration is the only measure which permits comparisons with other experiments to be made. The use of this ratio is open to some objection, since it assumes that changes in the environment have equal effects on both leaf and atmometer (**11**). In the experiments described here the transpiration was measured over short intervals of time so that this error was reduced to a minimum. *Kochia sedifolia* was used as a test plant in each transpiration series, and the ratio of relative transpiration remained constant under each set of conditions. Transpiration was measured as grams of water lost per square decimetre of leaf area per hour, and evaporation by using a standard Livingston atmometer of the white spherical type.

The transpiration was measured, using potted plants, by the potometer method and by measuring the rate of water loss of cut shoots at 5 min. intervals for half an hour after cutting. By the latter method it was found that the transpiration rate during the first 5 min. interval was higher than that of the subsequent intervals. It is possible that this is a traumatic effect, as comparison with potted plants showed that the initial rate of the cut shoot was higher than that of the potted plant. The transpiration of the potted plant corresponds closely with that of the cut shoot after the first 5 min. interval.

In the work described here the characteristic plants of the different communities have been selected and their transpiration measured. Account has been taken of the mean relative transpiration of the group rather than that of individual plants.

Wilson (**30**) has investigated the transpiration of potted plants during one day in summer and one in winter. These plants were from the sclerophyll forests and from the rain forests of Victoria. Wilson drew no conclusions from his work. We have analysed his results and obtained the following values for winter and for summer transpiration (Table IX).

Table IX. *Mean transpiration of plants during one day in winter and one in summer.*

	No. of plants	Transpiration in gm. per sq. m. winter	summer
Rain forest plants	9	50 ± 4·4	260 ± 60
Sclerophyll forest plants	20	44 ± 4·8	188 ± 25

The winter means show no significant difference in transpiration between the two groups. The variation in transpiration from species to species in both rain forest and sclerophyll types during the summer day is so great that it is difficult to compare the means. The difference of means and the standard error of difference is 72 ± 65, so that as far as statistical treatment is of value, there is no significant difference in transpiration between the two ecological types.

There is considerable variation in sclerophyll plants from the Mount Lofty Ranges. In these plants transpiration was measured by the loss of water from cut shoots; this is shown in Table X.

Table X. *Transpiration of plants from sclerophyll forest, South Australia.*

(Average annual rainfall, 30 in.)

Species	Transpiration (gm. per sq. dcm.)	Relative transpiration
Eucalyptus leucoxylon	1·5980	0·3085
Acacia pycnantha	1·5280	0·2920
Hakea rugosa	1·3080	0·2500
Leptospermum myrsinoides	0·4222	0·0807
Calythrix tetragona	0·5200	0·0994
Hibbertia stricta	0·7310	0·1397
Atmometer	5·2300	—

This group of sclerophyll plants has a mean value for relative transpiration of 0·1946 ± 0·0900.

The transpiration values of plants from arid communities are given in Table XI.

The relative transpiration of the sclerophyll-leaved and tomentose succulent-leaved plants of the arid communities is 0·1194 ± 0·0242 and 0·0278 ± 0·006 respectively. The difference of means and the standard error of difference is 0·0916 ± 0·0251, indicating a significant difference in transpiration value between the two groups. Inspection shows that the transpiration rate is low in plants of the Shrub Steppe compared with the scrub plants; also it will be noticed that the variation in rate between different species of the tomentose type is relatively small.

Table XI. *Transpiration of plants from arid communities at Koonamore.*

(Average annual rainfall, 8·00 in.)

Species	Leaf	Method	Transpiration (gm. per sq. dcm.)	Relative transpiration
Casuarina lepidophloia	S.	Potometer	0·0900	0·2000
Geijera parviflora	S.	,,	0·0193	0·0430
Eremophila scoparia	S.	,,	0·0565	0·1255
Atriplex vesicarium	T.	,,	0·0224	0·0500
Rhagodia Gaudichaudiana	T.	,,	0·0135	0·0300
Kochia sedifolia	T.	,,	0·0124	0·0280
Atmometer			0·4500	
Eremophila glabra	S.	Potometer	0·0617	0·0951
Acacia aneura	S.	,,	0·0545	0·0841
A. Victoriae	S.	,,	0·1610	0·2484
Kochia planifolia	T.	,,	0·0336	0·0518
Atmometer			0·6480	-
Kochia sedifolia	T.	Potted plants	0·0094	0·0303
Atriplex vesicarium	T.	,,	0·0093	0·0300
Atmometer			0·3102	
Kochia planifolia	T.	Cut shoots	0·1300	0·0510
K. sedifolia	T.	,,	0·0745	0·0292
Myoporum platycarpum	S.	,,	0·0900	0·0366
Atmometer			2·5500	
Acacia Burkittii	S.	Cut shoots	0·8102	0·1188
Myoporum platycarpum	S.	,,	0·2700	0·0400
Atriplex vesicarium	T.	,,	0·1470	0·0215
Kochia sedifolia	T.	,,	0·2000	0·0300
Bassia paradoxa	T.	,,	0·0850	0·0124
B. obliquicuspis	T.	,,	0·0470	0·0068
Zygophyllum fruticulosum	G.	,,	0·4551	0·0666
Z. prismatothecum	G.	,,	0·4012	0·0587
Atmometer			—	

S.—sclerophyll leaf; T.—tomentose succulent leaf; G.—glabrous succulent leaf.

Wilson (**30**), in one series of experiments with plants from the wet sclerophyll forests of Victoria (annual rainfall more than 40 in.), records values for the evaporation. On working out the relative transpiration from his figures one finds a mean value of 0·1559 ± 0·0514.

Firbas (**5**), in his investigations on the water relations of plants from the Hochmoor of Germany, gives values for transpiration and evaporation during the midday hours from which the relative transpiration can be calculated. These are as follows: *Vaccinium uliginosum*, 0·0905; *Calluna vulgaris*, 0·0800; *Empetrum nigrum*, 0·0566; *Vaccinium oxycoccus*, 0·1375; *Andromeda polifolia*, 0·0905.

The values for the mean relative transpiration in the foregoing groups of sclerophyll plants and tomentose plants are summarised in Table XII.

Table XII.

	Author	Relative transpiration
1. Sclerophyll-leaved plants		
Wet sclerophyll forest (Australia)	Wilson	0·1559 ± 0·0514
Dry sclerophyll forest (Australia)	Wood	0·1946 ± 0·0900
Desert Scrub (Australia)	Wood	0·1194 ± 0·0242
Hochmoor (Germany)	Firbas	0·0910 ± 0·0252
2. Succulent-leaved plants		
Shrub Steppe (Australia)	Wood	0·0278 ± 0·0067

If the relative transpiration of any of the four groups of sclerophyll plants are compared by the difference of their means it will be seen that in no case is there any significant difference in transpiration. On the other hand, the transpiration of the tomentose succulent-leaved plants is relatively and absolutely low when compared with any of the groups of sclerophyll plants.

It is evident from these results that the mean transpiration value in any group of plants with non-succulent leaves is approximately the same. This conclusion is at variance with that of Maximov (**15**) but adds support to the view of Stocker (**28**) that great variation in transpiration is found in any group of plants.

The tomentose succulent-leaved plants form a group apart from those considered here, and agree with the stem succulents in possessing an intrinsic low transpiration rate.

A clear distinction must be drawn between the tomentose succulent plants of the Shrub Steppe and certain glabrous succulent-leaved plants which occur in the same community. The latter plants belong chiefly to the genus *Zygophyllum*; seven species of this genus are found commonly in arid Australia. All of these are annual plants with the exception of *Z. fruticulosum* which occurs only in wetter soils. These plants are drought-escaping plants and are not members of the perennial vegetation. The transpiration values of these plants, shown in Table XI, are high, as is generally the case with the more mesophytic annual plants.

OSMOTIC PRESSURE.

The osmotic pressures of various desert plants, measured by plasmolysis in KNO_3 solutions, are given in Table XIII. The tissue investigated in all cases was the mesophyll. Braun-Blanquet and Walter (**3**) have pointed out the discrepancy which sometimes exists between the values obtained by the plasmolytic and cryoscopic methods, but it is not possible to use the latter method with the Chenopodiaceae which accumulate large quantities of salt in the epidermal vesicles. This renders the expressed sap useless for the determination of osmotic pressure.

The high values for osmotic pressure are in agreement with those found by Fitting (**6**) and Harris (**8, 9**). These high pressures are probably an intrinsic property of desert plants generally. The values for the woody plants are

Table XIII. *Osmotic pressure of arid plants, September,* 1931.

Species	Osmotic pressure atmospheres
Sclerophyll-leaved	
Acacia aneura	68
A. Burkittii	55
Eremophila scoparia	50
Myoporum platycarpum	43
Tomentose succulent-leaved	
Atriplex vesicarium	50
A. spongiosum	55
Kochia sedifolia	43
K. planifolia	35
K. triptera	47
K. pyramidata	47
K. tomentosa	38
Bassia obliquicuspis	47
Glabrous succulent-leaved	
Zygophyllum fruticulosum	10
Z. prismatothecum	7
Lycium australe	8

slightly higher than those for the tomentose succulent-leaved shrubs although the difference is not great. In their high pressure the plants with tomentose succulent leaves differ from the stem succulents which have low osmotic pressures (**9**). On the other hand, the glabrous succulent-leaved plants such as *Zygophyllum* and *Lycium* have low osmotic pressures. The osmotic pressures of plants with sclerophyll leaves from the Desert Scrub are higher than those found in sclerophyll plants from the Mount Lofty Ranges. The pressures obtained in the five commonest species in one forest type are shown in Table XIV.

Table XIV.

Species	Osmotic pressure atmospheres
Eucalyptus odorata	30
Acacia pycnantha	25
Hibbertia stricta	21
Xanthorrhoea semiplana	15
Leptospermum myrsinoides	18

These values are comparable to those of the Mediterranean plants described by Braun-Blanquet and Walter (**3**).

The success of the tomentose succulent plants in the driest areas in arid Australia is in large measure dependent upon suction pressure. The epidermis of these plants is uncutinised and in most cases absorbs considerable quantities of water from a nearly saturated atmosphere.

The cause of high osmotic pressures in desert plants is somewhat difficult to analyse. In the genus *Atriplex* it has been shown (**23**, **33**) that the cell sap is concentrated and consists chiefly of chlorides—usually from 10 to 20 per cent. chlorine as mixed potassium and sodium chloride on a dry weight basis. Calculations of the osmotic pressures exerted by the soluble salts present showed 65 atmospheres for *Atriplex paludosum* and 40 atmospheres for *A. vesicarium* (**33**). These values are in close agreement with those found by the plasmolytic method, so that it is probable that the salts are responsible for the pressures observed. In *Atriplex* there is considerable selective permeability, since the plants are not halophytes and the average Cl content of the soil horizon into which the roots penetrate is only 0·01 per cent.

In the cylindrical-leaved succulents the percentage of soluble salts is low, the average Cl content being from 2 to 3 per cent., and the bulk of the ash, like that of the stem succulents, consists of lime (**10**).

It has been shown that the tomentose succulent plants contain considerable percentages of pentosans as biocolloids and the osmotic pressure is probably complicated by imbibition effects.

SUMMARY.

The leaf types of the xerophytic plants of Australia fall into two groups—the sclerophyll leaf, characteristic of all climates except that permitting rain-forest development, and the tomentose succulent leaf, typical of the dry Shrub Steppe with low and uncertain rainfall.

In plants with sclerophyll leaves the mean stomatal frequency of any group shows no significant variation from any other group of plants from different habitats, with the exception of plants from the Shrub Steppe. Plants from rain forest in Australia or from British woodlands have the same mean stomatal frequency as plants from Australian sclerophyll forests.

In plants from the Shrub Steppe the stomatal frequency is low. Variations in stomatal frequency appear to be connected with generic and family characters rather than with varying environmental conditions. The percentage of stomata on both surfaces of the leaf apparently increases with increasing aridity of the environment.

Within the group of sclerophyll plants relative transpiration is extremely variable and the mean value of this ratio is not significantly greater than in any other group which has been examined. Plants with tomentose succulent leaves have a low relative transpiration compared with other groups of plants, and in this respect resemble the stem succulents.

The osmotic pressures of sclerophyll plants from arid communities is higher than those of sclerophyll plants from the forest areas. The pressures of plants with tomentose succulent leaves, unlike those of stem succulents, is high. In these plants part of this pressure is due to a high concentration of soluble salts and part to the presence of pentosan colloids of high hydration capacity.

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NORTHERN RHODESIA; AN EXPERIMENT IN THE CLASSIFICATION OF LAND WITH THE USE OF AERIAL PHOTOGRAPHS

By CHARLES ROBINSON ROBBINS.

(*With Plates VI–XI, two maps in the Text and one folding map.*)

CONTENTS.

PAGE
I. Introduction 88
II. Results 90
III. Conclusions 91
IV. Methods of work 91
V. Selection of types 93
VI. Maps 94
VII. Description of the area . . . 94
VIII. Climate 96
Appendix I. Growth types . . 97
Appendix II. List of species . . 104

I. INTRODUCTION.

THE Aircraft Operating Co., Ltd., at the time when aerial surveys of considerable areas of Africa were first mooted, put forward proposals for the production of a small-scale map with which would be combined a reconnaissance ecological survey. For these purposes a combination of oblique and vertical aerial photographs was proposed. It was further suggested that those areas which the reconnaissance survey showed to be more promising from the economic view should be completely covered with vertical aerial photographs. From these verticals large-scale maps would have been prepared which would have served as the basis for the more intensive investigations of the experts concerned with the development of the mineral, forest and agricultural potentialities.

The results would have been: large areas mapped cheaply and quickly on a small scale; the elimination during the reconnaissance of those areas which, for immediate purposes at least, were of lesser economic interest; the mapping of the more important localities on a larger scale; the confinement of the labour of expert investigation to those areas more likely to yield profitable results; and from all the above adequate data on which to base the policy and method of development for any particular area. The general result would have been that each area would have received attention in direct proportion to its importance.

Actually contracts were entered into for the mapping on a scale of 1/250,000 of an area of 63,000 square miles in the north-west of Northern Rhodesia. No arrangement was made for the use of the aerial photographs for an ecological survey.

The mapping under these contracts was approaching completion when it was suggested that, no ecological survey having been undertaken, the opportunity should be seized for the investigation of the possibilities of such a survey with the use of aerial photographs over an experimental area. The Government of Northern Rhodesia readily agreed to this proposal and selected the strip adjoining the railway between Kafue and Chisamba.

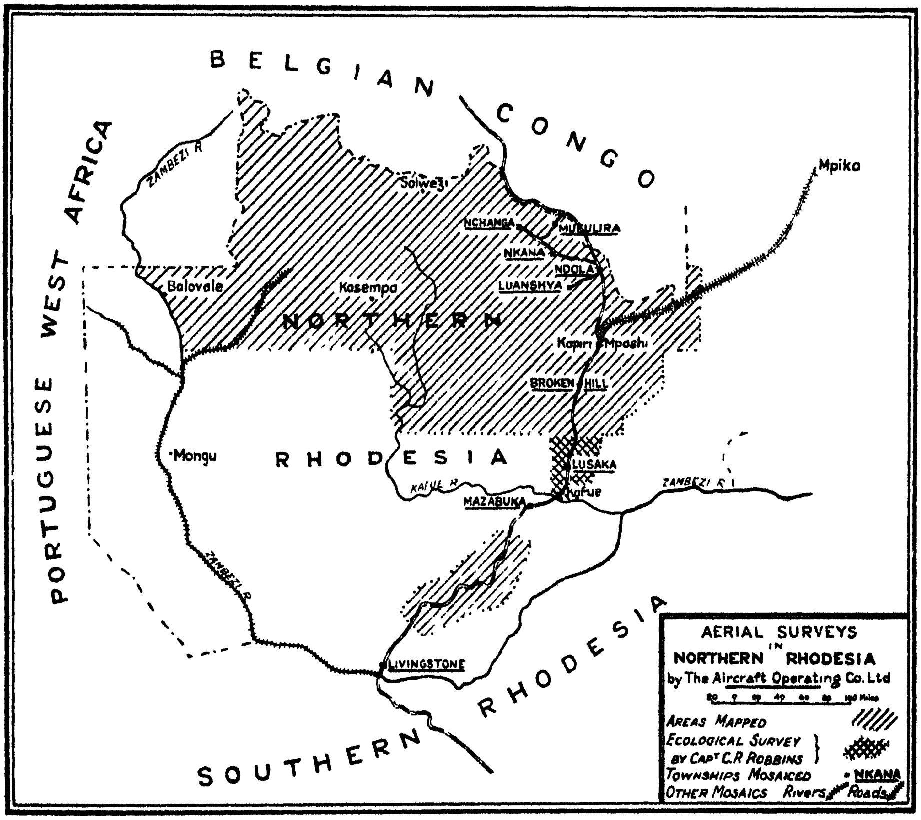

FIG. 1. Sketch-map of Northern Rhodesia, showing the area covered by the ecological survey.

The writer, supplied with the necessary oblique and vertical aerial photographs, was accordingly attached to the Agricultural Survey Commission for three months from the middle of August to the middle of October, 1931. During this period he rejoined the Commission's camp at intervals to ascertain their methods of working. The Commission, however, was more concerned with the valuation of actual or potential individual farm sites and, moreover, did not concern itself with any native reserve. The writer, on the other hand, perforce regarded the whole area as subject to the experiment and was indifferent, except insomuch as his classification affected it, to the existing economic or political status of any particular locality. Indeed, the area involved was regarded exactly as some more or less unknown region, e.g. that between the Kabompo and Zambesi rivers, would have been regarded, that is, absolutely empirically.

It should be made plain that the whole subject of this report was experimental. The writer had no previous knowledge of the nature of the area, and although he had had considerable experience with the use of vertical aerial photographs for forest stock-mapping, he had never before tried such work with obliques. It was therefore not known at the outset what actual results could be achieved, though it was certain, by analogy from similar work elsewhere, that these would be of value. Given an ecological survey of this nature, but covering an area sufficient to justify the employment of specialists, it is certain that better results would be achieved than where one individual had to supply, in the field, the botanical[1], soil and geological background for his observations. The writer has only the general, practical knowledge of these subjects such as is common to all trained forest officers of experience. He can claim, however, a very extensive experience indeed in the interpretation of aerial photographs. This is mentioned only because the study of aerial photographs presents great difficulties to those not fully initiated.

II. RESULTS.

In actual fact during the three months in the field the following results were attained:

Nearly 3000 square miles were covered, which gives an average production of about 50 square miles a day, allowing for days occupied in rest, writing up data, moving camp, etc. No method, other than aerial sketching (in which the boundaries are not so accurate), not using aerial photographs, can approach this for speed.

Eight types and twenty-five sub-types were distinguished on the ground and on the photographs, and the boundaries transferred to a map. The identification on the ground, without the use of aerial photographs, of the entire length of all those boundaries would have been an immense labour and would, moreover, have demanded years of ground survey to have placed them reasonably accurately on a map.

From the maps on which these boundaries have been marked there can be picked out with absolute certainty those areas:

(*a*) Containing the highest proportion of the better class arable lands[2] and which are, therefore, those areas which should first form the object of expert investigation as likely to provide sites for European settlement, type VIII.

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[1] The writer is much indebted to Mr Duncan Stevenson, Senior Assistant Conservator of Forests, for his valuable help in the determination of the identity of many tree species.

[2] It should be noted that while cleared fields may indicate better land it is in such areas that classification was most difficult, as much of the evidence, i.e. original tree growth, has been removed or altered by past or present cultivation.

(*b*) Where arable land exists but in smaller blocks and mixed with sites more suitable for pastoral purposes, type VII. Or with a soil of very variable depth and often with heavy bush, type VI.

(*c*) Of flat forest on limestone, flat forest on sand, and hill forest on shale, etc. (that is, types V, IV, and III) which are largely useless for all agricultural purposes. It is, however, possible to delimit the boundaries of those forest areas which should be protected in the interests of the future water supply.

(*d*) Many types of grassland, with or without trees, which are subject to water-logging.

A great deal of information concerning the forests and geological formations.

III. CONCLUSIONS.

It is considered that the results embodied herein and in the attached maps prove definitely that reconnaissance ecological survey, allied with the use of aerial photographs, can:

(*a*) Rapidly indicate the situation of those areas of greater interest and at such a cost that the subsequent saving of the time of the experts would more than recoup the initial outlay.

(*b*) Provide a mass of other information most of which can be marked on a map. Such information can therefore be checked how and when desired, which is not generally true of the generalisations produced by primary surveys of any kind.

It is also considered that were, as has been suggested, the more important areas covered with vertical aerial photographs for the preparation of larger scale maps, an intensive study of these photographs would yield valuable results. Even where the information required can be gained by study on the ground only, photographs are immensely useful as field-maps, providing such a mass of detail that all boundaries, types, sites, and particular points can be marked with accuracy and certainty.

IV. METHODS OF WORK.

At the outset nothing was known by the writer of the geology, soils, growth types or the habits of the plant species in the area. Nor had anything been read about them, as it has always been his experience that it is best to approach such problems with a mind completely unprejudiced by previously expressed opinions.

Accordingly, when the survey was started at Kafue in August, 1931, the writer accompanied the Agricultural Survey Commission on their excursions and also made excursions of his own. During these preliminary journeys no attempt was made at any classification, but the localisation of the commoner tree species was noted and marked on the prints—until such time as the various growth types appeared to become differentiated on the ground and recognisable on the prints.

When this stage was reached the ideas formed were submitted to a close scrutiny by selecting photographs of areas not yet visited; deciding what types they appeared to bear and where the boundaries lay: and then going to the actual area to ascertain to what extent these conjectures were correct.

After it had been definitely established that any particular appearance on the prints was correlated with a growth type, all areas having that appearance were assumed to be of that type. Thereafter, in such localities, those parts only which provided some doubt were visited, and such journeys automatically gave further tests of the known types as areas of them had to be passed.

This process had to be repeated wherever the photographs passed from one general region to another; for example, at the break from the steep shale hills east of Kafue to the mixed limestone-sandstone-quartzite broken country and thence into the limestone plateau of Lusaka.

As a general rule efforts were made to go completely over the ground covered by the strips of vertical photographs. These follow the railway line and run parallel to it, at an average distance of 10 miles on each side except between Lusaka and Kafue, where they are on the east side only. The results provided by the study of these were transferred to those parts of the obliques covering the same area and thence, by similarity of appearance, to the areas covered by obliques only. But to reach the flank verticals necessitated passage over country covered by obliques, and all such opportunities were seized for further check. Moreover, puzzling areas on the obliques themselves had to be visited.

The line of flight of the oblique photographs was practically the same as for the verticals, but the exposures were made obliquely at about one-minute intervals, first to the right, then to the left, and then to the rear. The obliques in any one line not only overlap in themselves but also, on the sides, look at the same ground, from the opposite view, as the neighbouring line of the obliques. Thus, except at the outer edges, many parts are covered two or three times from various angles, which in itself provided a check on the interpretation.

The work proceeded spasmodically: being slow when the outskirts of a new region were encountered and becoming more rapid as the characteristics of the tract were comprehended.

All photographs had been taken from an altitude of 10,000 feet above the average height of the ground. A 7-in. lens was used which gave a scale on the vertical prints of about 3¾ in. to the mile.

It should be noted that while the obliques, even on those parts where the scale is largest, cannot compare with the verticals for the amount of detail provided, they have the great advantage of showing up clearly main boundaries which on the verticals are obscured by the very excess of detail.

V. SELECTION OF TYPES.

Although, as has been explained in the method of working, certain growth types were established and recognised during the field work, it was not until the mass of information, comments, boundaries, etc., marked on the prints had been collated that a conception of the growth over the whole area was possible.

It was then found that certain forms repeated themselves within a type and were sufficiently distinctive and extensive to be assigned to sub-types: for example, the three grades of swamp grassland.

Moreover it became plain, on examination, that other areas, which, in the field, had by reason of their complexity appeared to offer insuperable difficulties to any classification showed several distinguishable forms that were repeated constantly and thus permitted their allocation to a type containing these as local variations. Such areas are those of VII where the great variations of slope, soil depth and particularly underlying rock provide conditions for many growth forms. These, by repeating themselves over and over again, provided a whole of which they formed a part.

Also areas, of which the allotment in the field had been obscure, were found to fall naturally into their places as transition zones once a general view of adjoining areas was available on a map.

The greatest difficulty in the selection of the type was experienced in those parts where past and present cultivation and cutting for fuel has removed all or many of the trees.

The evidence of the natural crop having been destroyed it was not easy to discriminate the original growth forms in the resulting scrub bush and artificial grassland.

It will be observed that the tree growth, being the natural feature most readily recognised on aerial photographs, has been largely used as the type-indicator. In spite of this it will be perceived that there is a very definite correlation of the types with the moisture, soil and rock conditions present.

I, II. Alluvial, shallow soil, excess water.
III. Shale hills, much rock, good drainage.
IV. Sandstone—sand undulations, varying soil depth and drainage.
V. Limestone flats, shallow soil, poor drainage.
VI. Mica-schist, varying soil depth and drainage.
VII. Geological contacts, mixed rock and soil, fair drainage.
VIII. Colluvium, deep soil, good drainage.

Although the whole survey has been approached ecologically and due consideration has been given to the factors, climatic, edaphic, etc., affecting growth, no definite detailed study has been made to allot the types to plant communities nor to discover their successional relationships. The main object, a primary survey, has been kept constantly in sight. Anything likely to obscure this issue was studiously avoided. It is thought, however, that the types selected will fall into line with those adopted by such workers as J. Burtt Davy, J. S. Henkel and John Phillips.

VI. Maps.

The original topographical maps prepared for the Government of Northern Rhodesia by the Aircraft Operating Co., Ltd., were at a scale of 1/250,000. These were considered to be on too small a scale adequately to demonstrate the information secured. Accordingly enlargements were made to a scale of 1/50,000 which is the same as that commonly employed for farm maps, thus permitting direct comparison with the data obtained by the Agricultural Survey Commission.

The enlargements were prepared by the laborious process of gridding, and then detail, over and above that which the 1/250,000 maps could support, was added from the prints. Being a five-times enlargement the sheets produced cannot be considered strictly accurate. On this framework the type boundaries were marked. All boundaries have been shown by a full line other than where the mergence of types is indistinct (in actuality or on the prints) and on the edges of the area where the obliques have been used to their fullest possible range. A specimen is reproduced on the opposite page (Fig. 2).

Where clear, the sub-type boundaries have been drawn, but where they fuse by a gradual transition the sub-type numbers only have been used.

VII. Description of the area.

The area comprises a strip along the railway and is 30–35 miles wide between north of Chisamba and Lusaka, and 20–25 miles wide from Lusaka to Kafue. It lies in Northern Rhodesia between approximately latitude 15° and 16° south and on longitude 28° 30′ east. The altitude varied from 3240 ft. at Kafue to 3770 ft. at Chisamba, the chief rise of 750 ft. being between Kafue and the vicinity of Chilanga at 4000 ft. The highest ground is on the limestone area of Lusaka at 4200 ft. From here it falls to the north to 3490 ft. at the mission at Kasisi and rises slowly to fall once more to the valley at Chisamba. The part south of Lusaka is drained by the Kafue River and its tributaries: and north of Lusaka by dambos[1] and streams flowing generally east and west from the railway which largely follows the trend of the watershed. North of Chisamba the drainage area of the Mwomboshi, flowing east, is entered. The folding map shows a strip 20 miles wide, with geology, soil and vegetation separately represented.

Topographically the area falls into five main regions:

(*a*) A hilly country with steep slopes to the east and north-east of Kafue (Fig. 2).

(*b*) The flat alluvial plains of the Kafue River to the west.

(*c*) The limestone plateau of Lusaka.

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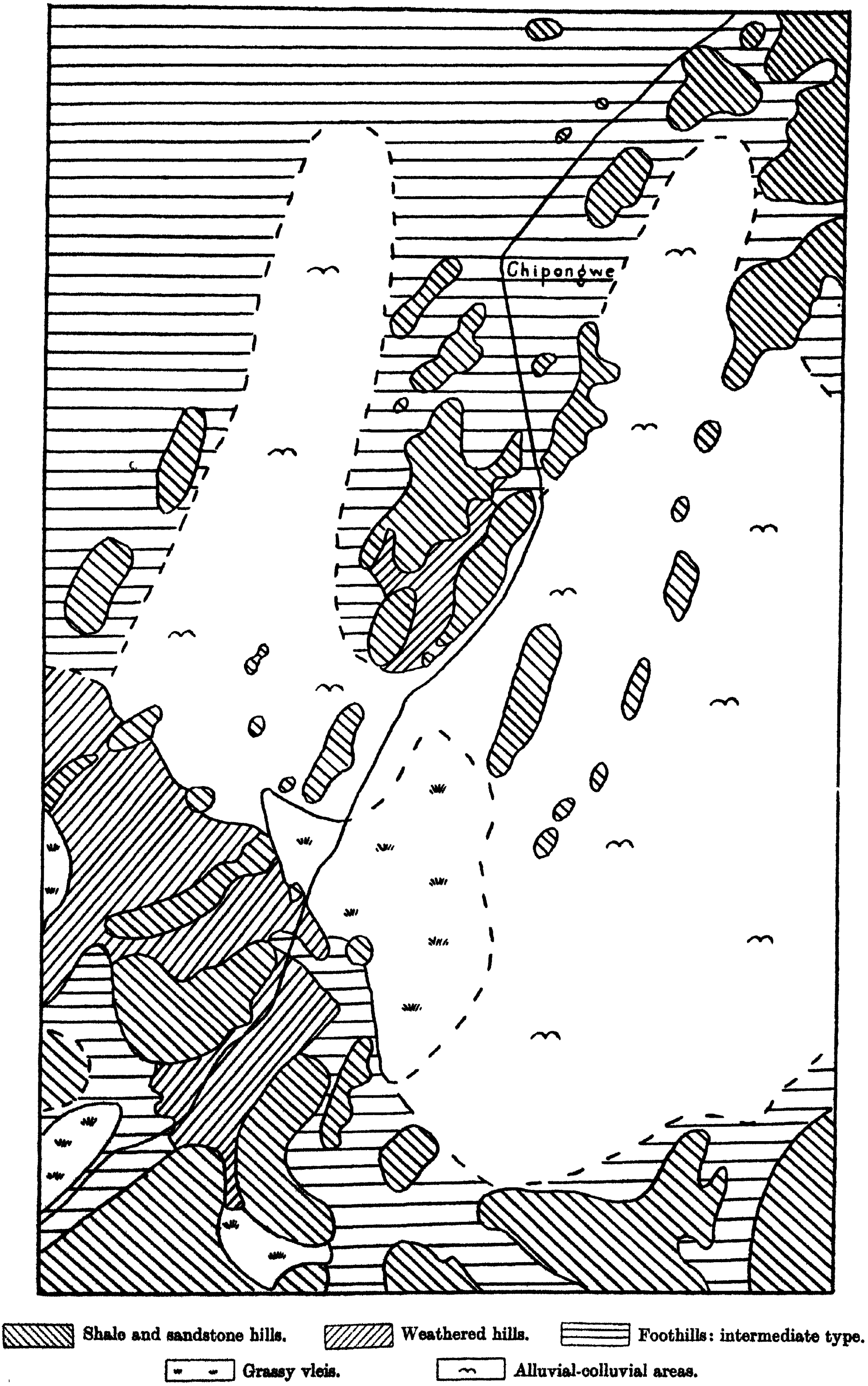
[1] Grassy areas, usually panned, which serve as channels for surface water.



Chipongwe
Shale and sandstone hills.
Weathered hills.
Foothills: intermediate type.
Grassy vleis.
Alluvial-colluvial areas.

(*d*) The peneplain, mainly flat and undulating and with few hills between Lusaka and Chisamba.

(*e*) The mildly hilly country of the Mwomboshi drainage.

Geologically much the same regions can be traced, but there are several subsidiary and contact zones which are of major importance (see Fig. 2 and folding map).

(*a*) The hills to the east of Kafue are of shale which passes still further east (outside the prints) into another rock which may be a granite or a sandstone. To the north-east these shale hills are intersected by deep valleys where the underlying limestone has been partially exposed.

(*b*) To the south of the limestone plateau on which Lusaka lies denudation of the shale-sandstone-quartzite has proceeded to such an extent that very broken country is met, with all these rocks occurring mixed with outcrops of limestone and ironstone and probably gabbro, and areas of alluvial and colluvial deposits.

(*c*) To the north and east of Lusaka the limestone disappears under quartzite hills but reappears where those hills fall into the flat area. To the north of this flat area, over much of which the rocks are hidden but which probably has gabbro, the limestone again disappears (and it is believed stops completely). Its place is taken by a micaceous, schistose rock (possibly the basement mica-schist) which, although outcropping freely, is much overlaid by quartzite on the west and middle: on the east there are large areas of sand under which it is believed there lies another rock which may possibly be a quartz-dolerite.

(*d*) On the southern edge of the Chisamba flat there are bands of conglomerate running east and west. On the northern edge the country rises to hills made, it is believed, of frequent and obscure alternations of quartzite and schist, with outcrops of ironstone. In the Mwomboshi valley itself, which lies outside the area, it is possible that the schists have been much exposed.

(*e*) Granite outcrops were found in a few places, but while their intrusion has probably been the cause of the intense distortion of many of the rocks their influence on the soil derived from the rocks as they now lie is probably negligible.

The plates represent specimens of the use of aerial photography in mapping soil and vegetation types.

VIII. CLIMATE.

The average rainfall for the whole area is about 35 in., being rather less at Kafue and rather more at Chisamba. There are very considerable fluctuations, a maximum of 58 in. having been recorded at Chilanga and a minimum of 18 in. at Lusaka. Most of this rain falls between November and March, though there may be showers, sometimes heavy, in October, April, and even May. There is a tendency for January to be the wettest month and together with December and February to supply two-thirds of the total rain. But there are also great fluctuations.

The hottest months are September–November with a mean daily maximum of about 90°: the coolest months are May–August with a mean daily minimum of about 50°. The mean daily range of temperature is greatest during the cooler months and the first part of the rains period. The mean humidity is highest in January–February when it is about 80, and least in September–October when it is about 45 $^{\circ}/_{0}$, just before the rains break. The prevailing winds are east to south-east and may attain considerable speeds at certain seasons, notably the drier warmer months of September and October.

APPENDIX I.

GROWTH TYPES.

I. Alluvial grass swamp	A. Riverside
	B. Black soil
	C. Dambo
II. Alluvial tree-grass semi-swamp	A. Mupane
	B. Mulama
	C. Munga
	D. Flood season
III. *Brachystegia* hill forest	
IV. *Brachystegia* plains forest	A. Local hills
	B. Kabunga, *Uapaca* scrub
	C. Flat or undulating.
	D. With large kabunga
	E. With mukoso
V. Limestone outcrops	A. Grass and scrub
	B. *Brachystegia* forest
	C. *Brachystegia*, etc., with deeper soil
VI. Mica-schist outcrops	A. Swampy with much mubanga
	B. With *Brachystegia*; local ridge
	C. Deeper soil, flat, red. creepers
VII. Second grade	A. Foothills
	B. Remnant rock
	C. Flat, red soil
VIII. First grade	A. Flat with various levels
	B. Deep residual soil on slight hills
	C. Colluvium with thorn.

Mr C. G. Trapnell has kindly added critical notes to some of the sections.

I. A. *Riverside swamp.*

This type is important locally only along the banks of the Kafue River before the stream enters the gorge. It comprises primarily three strips of varying width: those nearer the stream being always wet, even during the low-water level period, and that farther away being inundated throughout the period of normal high-water level. The sub-type farther from the river may provide useful grazing during the dry weather. The wetter are also of importance as preventing easy access to the water and the passage of animals. The wettest area supports aquatic and semi-aquatic plants and the two less wet a grass-reed growth. Trees are scarce and are chiefly represented by a very narrow strip of fringing forest which is of academic interest only. Such species as *Syzygium* sp., *Protorhus* sp., *Ekebergia* sp., and *Kigelia pinnata* together with *Ficus* spp. occur.

I. B. *Black-soil swamp*[1].

The main block of this type is to be found in the vicinity of Chisamba at the place where all the main sources of the Chongwe unite to form the actual infant river. The cover is of swamp grasses, the dominants being *Hyparrhenia rufa*, *Setaria phragmitoides* and *Setaria phleoides*. Very few trees are present, though in some cases these areas formerly carried trees of the bush group (now cut or burnt out) about the termite heaps which are scattered evenly over the areas, except on the lowest parts. These heaps are 3 to 4 ft. high.

Areas of this type include the more truly alluvial or colluvial reaches of the dambo system of this country. They occur extensively to the west of Kafue but are too far away on the obliques to be mapped. In the situations where this type occurs there exist also conditions permitting drainage, if this were ever considered worth while. Where the soil is a little more favourable and the run-off a little quicker, they are of importance as providing a reserve dry-weather grazing.

I. C. *Dambo.*

The term is restricted to the comparatively eluviated dambos of the upper reaches of the dambo drainage system, which are characterised by a sour, sandy and panned soil. Under this head have been included all those areas of grass-swamp which, owing to the flat nature of the terrain, take the place of streams in removing surplus water. This type covers very considerable areas, particularly to the east of the railway between Chikumbi and Chisamba. There are many sub-types (which could be separated by study of the soils and grasses) but all agree in bearing coarse grasses, including characteristic species of *Trichopteryx*, especially *T. simplex*, in having few trees and being badly panned to the extent usually of an impermeable layer of laterite-like rock a short distance from the surface. They are swampy throughout the rains.

The two main sub-types are the broad flat dambos, with large scattered termite hills bearing *Combretum splendens* and *Acacia* spp. which occur among and often merge into type IV, and the narrower areas with more sloping sides and commonly a definite stream bed which are restricted to the vicinity of frequent changes in the underlying rock. These narrow dambos seem to be associated, except in the really hilly parts, with alternatives or mixtures of IV and VI. They may have narrow strips of usable soil along the edges. At lower levels, or in regions not yet reduced to peneplain conditions, black-soiled alluvial dambos are found which formerly carried *Acacia campylacantha* trees, etc.

II. A. *Mupane semi-swamp.*

The main block of this type occurs on the inner bend on the south bank of the Kafue River, opposite to Kafue on alluvium laid down by the river; another occurs farther west on the north bank but is too far away to be mapped. A third small area lies to the south of Chisamba on ground slightly higher than the surrounding black-soil swamp. The soil is not always alluvial in this area. It is peculiarly subject to sheet erosion, leading to an appearance of scarcity of grass. Much of the ground is bare, being caked hard in the dry weather and water-logged in the rains.

Typically the mupane (*Copaifera mopane*) occurs nearly pure, in the less swampy ground, or is dominant with *Euphorbia cooperi* in the bush-group form about ant-hills further from the river. Still farther off both these disappear and are replaced by the species of II D. The undergrowth of the bush groups commonly consists chiefly of *Sansevieria cylindrica.*

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[1] This section and the following eight have incorporated in them notes made by Mr C. G. Trapnell and sent to the author.

In the small area near Chisamba both *Acacia campylacantha* and *Combretum splendens* occur with the mupane.

II. B. *Mulama semi-swamp.*

This type is really a transition between true treeless swamp and the adjoining forest type. Its boundaries are very arbitrary as it usually merges gradually into grass swamp or tree forest. In places it changes progressively to II C (as south-west of Chisamba) and in others to VI A; sometimes it is found on dambo edges.

Its chief importance lies in indicating swampy tendencies where no actual swamp may occur. The ground is sandy and more or less waterlogged in the rains owing to pan or rock near the surface. Mulama (*Combretum splendens*) and chibubu (*Terminalia torulosa*) are commonly co-dominant, with associated sour grass; but on rocky ground *Diplorrhynchus mosambicensis* is equally plentiful. In the area to the south-west of Chisamba where the surface soil is nearly pure sand the mulama is associated with *Protorhus* sp. *Afrormosia angolensis* and *Acacia woodii* occur but are not typical.

II. C. *Munga semi-swamp.*

Like II B this type also is a transition between swamp and drier land but it is almost restricted to strips between black-soil swamp and either mixture VI or else some form of drained, deep soil. The soil is frequently black, but gradually becomes browner and lighter as the passage is made to higher ground. Parts of such areas are likely, with drainage, to provide arable land or at least pasture. The narrow strip of VIII running east from the railway, to the south of Chisamba, approximates to this type but is nearer VIII A and accordingly has been so classed. The Munga (*Acacia campylacantha*) is the normally dominant tree, while the mukoka (*Acacia woodii*) occasionally occupies sandy swamp soils in this area. *Acacia hebecladoides* and *Albizzia harveyi* are typical associates, and either may be dominant over smaller areas. Ant-hills are plentiful.

II. D. *Flood season.*

This type is of small extent and like II B and II C is a transition but it is restricted to areas lying between the riverside-mupane areas and the foothills VII A: though small blocks of similar nature are found in VI A. The areas are probably not actually flooded but the run-off is so slow and the water-table so high that conditions equivalent to flooding are produced.

The principal tree species are *Euphorbia* spp., *Terminalia* spp., *Combretum* spp., figs and some *Bauhinia.* Mupane is absent. Such species as *Diospyros* and mukanongo (not identified) may also occur and a few thorn trees on local rises. There is a dense undergrowth of grass, probably mainly *Hyparrhenia* sp. The large flat areas known as the Kafue Flats are not included as they lie outside the area mapped. These are now largely treeless except for scattered palms, but it is possible that man and fire are responsible for this state.

III. Brachystegia *hill forest.*

Very considerable areas are accounted for by this type which covers hundreds of square miles on the east of the railway between Kafue and Lusaka. The main characteristics are those of a definitely hilly country, with slopes moderately to very steep, covered with bush, the dominant trees being *Brachystegia tamarindoides,* and, at the sandy hill-foot *B. hockii. B. filiformis* is present but does not ascend far up the rocky slopes. The canopy is fairly complete and the grass growth light.

To the east and north-east of Kafue the allotment to this type was simple as the red shale hills (probably granite as shown by their more rounded shape and smaller individual size) are equally prominent. But more to the north, where hills and flat or undulating country are mixed, the decision as to whether some areas belonged to this or to IV A or IV C has been necessarily arbitrary. To some extent this has been overcome by creating the sub-type IVA.

From the arable point of view all this type is completely useless, the soil being thin and the slopes steep. Rock outcrops are many. It is possible that better grass might be produced by cutting some of the tree growth, especially on the flat tops, local level places and at the foot of the hills where the soil, mainly sand, has accumulated to a greater depth and bears almost pure *Brachystegia filiformis.*

Some outlying hills, so situated or so weathered that they might have been included in VII A, or even VII B, IV A, or IV C, have been put under this head on account of the presence of definite rock outcrops. On the talus *Kirkia acuminata* is the chief tree, with *Pterocarpus angolensis* among scrub of *Commiphora.*

IV. A. Brachystegia, *local hills.*

This is distinct in composition from III. *Isoberlinia globiflora* is most commonly dominant along the crests of the hills, while in some parts *Brachystegia filiformis* is dominant, and *B. hockii* is present on the surrounding sandy slopes or flats.

Otherwise this type is much as III, some indeed of the more definite hills, surrounded by flatter bush, have been marked as III.

IV. B. *Kabunga,* Uapaca *scrub.*

This type does not cover any very large area, though there is a considerable extent of it in the vicinity of the swamp south of Chisamba and along the large dambo to the north. The general level is raised very little above that of the neighbouring swamp, this rise in level is generally caused by outcrops of quartzite or conglomerate; the soil is almost pure sand. Growth is stunted: possibly averaging 12 ft. in height. *Isoberlinia globiflora* with *Uapaca nitida* and *U. Kirkiana* are the most frequent trees.

IV. C. Brachystegia, *flat or undulating.*

Together with III this type comprises a great part of the total area. It differs largely from III in that hills are absent and that such outcrops of rock as do occur are almost invariably found at the tops and the bottoms of the slight slopes. Generally the type consists of vast flat or undulating areas of sand. The canopy is fairly dense, permitting only light grass. The composition differs little from the preceding sub-types, and the principal tree species are *Brachstegia filiformis* and *B. hockii* with *Isoberlinia globiflora* becoming more and more common to the north. The flattest parts have sometimes an almost pure crop of *B. filiformis.*

Growth varies considerably: where this type abuts on VI it is much better than in the large areas to the east of Karubwe and to the north of Chisamba. Much of the type has been subjected to shifting cultivation and it is probable that the soil is such as to permit no other form. Included in this type are the flat plateaux which occur on the tops of the hills to the north-east of Kafue. These have been much cultivated.

IV. D. Brachystegia *with large kabunga.*

This particular sub-type is almost identical with IV C and is found in those flat areas adjoining VI B and C. Its only importance lies in the fact that the soil is rather better, being redder, less sandy and a little deeper. It frequently merges into VI B and in places is inextricably mixed with it.

IV. E. Brachystegia *with mukoso.*

On the east, to the north of Chongwe River, there is an indefinite area in which the *Brachystegia hockii* becomes less common and is partially replaced by *Erythrophloeum africanum*. The soil is still very sandy but it is better and has been much used for native cultivation.

V. A. *Limestone, grass and scrub.*

Where the limestone outcrops very close to, or actually at, the surface there are found areas of scrub and stunted growth intermingled with grass. The grass may provide some grazing. but the chief interest in these areas lies in the patches of *Protorhus* sp., *Syzygium* spp., *Royena paliens* and swamp thorns which mark the site of perennial springs. The grasses are also of interest as, in places, there are species of mat as opposed to the common turf grasses. Most of the limestone outcrop to the west of Lusaka is of this type, though the limestone and the resultant growth is confused in many places by remnants of sandstone and quartzite.

Economically the area is of little interest apart from the obvious necessity of protecting the tree growth to maintain the springs. Ecologically it would provide much matter of botanical interest if studied closely: but in a reconnaissance survey no true indicators appeared other than the general scrubbiness of the growth.

Mr C. G. Trapnell notes: "This is nothing more nor less than the mulama type described above (II B), occupying an eluviated soil full of iron nodules, and damp during the rains. It has abundance of *Diplorrhynchus mosambicensis*, associated with the rocky soil, and of *Pseudolachnostylis*...."

V. B, C. *Limestone and with* Brachystegia.

Where the limestone is not so near the surface and the soil becomes redder and deeper there appears a growth of *Brachystegia filiformis* and *B. hockii*. Limestone outcrops are still frequent but there are patches of better soil, and locally these may occupy several acres. Except where shifting cultivation indicates them, the best patches cannot be found except by actual inspection. Generally the Lusaka belt improves from west to east and the deepest soil is found where the limestone band is narrowest. Where the soil is becoming deeper such trees as *Bauhinia*, *Diplorrhynchus mosambicensis* and *Afrormosia angolensis* are found mixed with the *Brachystegia*. In still deeper soils some *Albizzia buchananii*, *Pseudolachnostylis glauca* etc. may be added.

VI. A, B, C. *Mica-schist outcrops.*

The outstanding feature of this type is that it is almost invariably found on a red soil overlying a rock which is both micaceous and schistose (Pl. VII, no. 02219). Typically, as shown at its best for example in VI C, the number of tree species is great and they are thoroughly mixed. Moreover, although grass may be present, the more usual undergrowth is a thicket of small shrubs, trees, coppice, etc. which, in places, becomes so matted together by creepers as to be wellnigh impenetrable. Over much of the best sub-type the soil is quite capable of being used for arable farming but the initial clearing would be expensive.

Where the areas tend to become low-lying *Afrormosia angolensis* becomes very common—but badly shaped—and the soil is paler in colour and heavier in texture (VI A). In some areas, notably between the Great North Road and the railway north of Karubwe, it would appear that the alternatives of quartzite and schist are so frequent, or the resultant soils so mixed, that the already very mixed crop becomes even more intermingled with *Brachystegia hockii* and *Isoberlinia globiflora*, changing into IV D. The large area to the north of the block of VIII, on the west of the Great North Road, is made up of areas of all three sub-types of

VI; this might be expected as it lies along one of the main geological changes where the basement schists, here exposed, are covered to the south by limestone and to the north by quartzite.

The best soil in this type is to be found north-west of the Kasisi Mission where also the limestone makes its last appearance. The area of VIII north of the mission also approximates to VI C but is so good locally that it has been put in the better type.

With regard to this type Mr C. G. Trapnell remarks: "The vegetation which has been described under this head consists of (*a*) forms of *Brachystegia-Isoberlinia* bush on the poorer sandy soils, (*b*) *Combretum-Afrormosia-Albizzia* bush on the better sandy soils, and (*c*) a dense scrub variation of the last with *Combretum* spp. and creepers occupying caps of residual red soil with or without outcrops. The *Combretum-Afrormosia-Albizzia* bush is found on Limestones, Hook Granites, shales, Kalahari sands etc. outside of this area. Characteristic trees in this area include *Afrormosia angolensis*, *Combretum Zeyheri* and spp. *Dalbergiella Nyassae*, *Lonchocarpus capassa*, *Albizzia*, *Terminalia*, *Vitex*, *Erythrina*, *Burkea* and *Schrebera* spp.... For a single name it is best known as mubanga (*Afrormosia*) country. In parts it has been considerably altered by selective felling, the mubanga and *Albizzia* poles being much used for native huts, and *Combretum* spp. may be then dominant."

VII. *Second grade.*

As its name implies this is not a real growth type but is an artificial type made to include all those areas which contain some potential arable land but which are not good enough or large enough to be included in VIII. Generally it will be found that this type is confined to those areas where there are outcrops of many different rocks and many small hills, some of one rock and some of another. Typical examples are around Chilanga where sandstone, limestone, quartzite, gabbro (?) and possibly other rocks occur within a few yards of one another. The true foothills type, VII A, is to be found where the hills to the north and north-east of Kafue have been denuded to form valleys. The soil consists of recent hill-wash and it is probable that a state of equilibrium has been reached where the new soil washed on is balanced by soil washed off.

Sub-type VII B is found typically in the jumble of rocks and small hills around Chilanga: to the east of Lilayi: and in valleys of the upper tributaries of the Funswe River. The variation in rock and soil is frequent and abrupt as might be expected where the sandstone-quartzite hills have been denuded, leaving caps of varying thickness over the limestone which is in turn pierced by outcrops of gabbro. The tree species are much the same as in VII A but there are more and the variation from place to place is more abrupt. Areas of this type contain many small patches of deep colluvial soil which are not large enough to be mapped but which, in the aggregate, constitute a not inconsiderable whole. Moreover, some of the hill tops and slopes also have deep soil. It is probable that much of the area not utilisable for arable farming could be used for pastoral purposes.

The last sub-type, VII C, occurs among VII B, but it has been selected to show those areas where the process of denudation has proceeded farther and, instead of the small hills and rock caps, the flatter areas in between predominate. It occurs in its most typical form to the north of the Star Mine: here there are flat ridges of remnant sandstone-quartzite running east and west over flat areas of limestone. These flat ridges vary from IV C on the tops to VII at the sides. At the bottoms there are areas of red soil overlying limestone. Some of the soil in these areas approximates to type VIII with thorn; but elsewhere and locally the presence of *Erythrophloeum africanum* and *Pterocarpus angolensis* suggest sand, while *Combretum splendens* suggests poor drainage and shallow soil. There are some areas of actual limestone outcrop with poor scrub, V A, but these are too small to be mapped.

It is difficult to select the typical tree species as so many soil sites are found in this artificial class. But it is probable that the *Albizzia* spp. and *Lonchocarpus capassa* would apply to the better areas of VII C.

Mr C. G. Trapnell observes: "...Much of this ground consists of *Combretum-Afrormosia-Albizzia* country of the better *Albizzia stuthiophylla* type, and indistinguishable in composition from the last. In other cases inliers of thorn bush have been included. If any distinction needs drawing, it is a subdivision of the mubanga (*Afrormosia*) country whose three main variations, *Erythrophloeum* form, *Combretum-Afrormosia* bush proper, and *Albizzia* form have already been noted."

VIII. *First grade.*

This is another artificial type in which have been collected all those areas which contain the main blocks of potentially arable land. Sub-type VIII A is found typically in the wide valley of the Maluto river, north-east of Chipongwe, and more so in the area straddling the Great East Road on the east of the Ngwerere River. In such areas there are very considerable tracts of colluvial soils suitable for agriculture, but there are also many patches where the land is too low to be useful without extensive and difficult drainage, and many others on slight rounded hills, where there may be too much broken rock and pebble left. All these different classes could probably have been separated were it not that the action of man, both by shifting cultivation in the past and by European farming in the present, has, with the natural growth, removed all the evidence and converted all alike to grass-land which shows little differentiation in the oblique prints. Where the rounded hills included in VIII A are sufficiently extensive and bear generally an adequate soil, their presence has been marked as VIII B.

The most important sub-type, VIII C, includes all those areas of colluvial soil which are reasonably well drained and can be cultivated without great initial expense, as much of the bush has been removed by past cultivation. As a general rule all such areas, except in the native reserves, already bear European farms. But the presence of ploughed lands is no true indicator of the best soil, as some original fields, now abandoned but still visible, were started where initial clearing was least. There are also examples of other factors, e.g. proximity to a town or the presence of water for irrigation, causing land classified as VII (just north-east of Lusaka) or even as IV C (wheat fields to the north-west of Lusaka) to be cultivated.

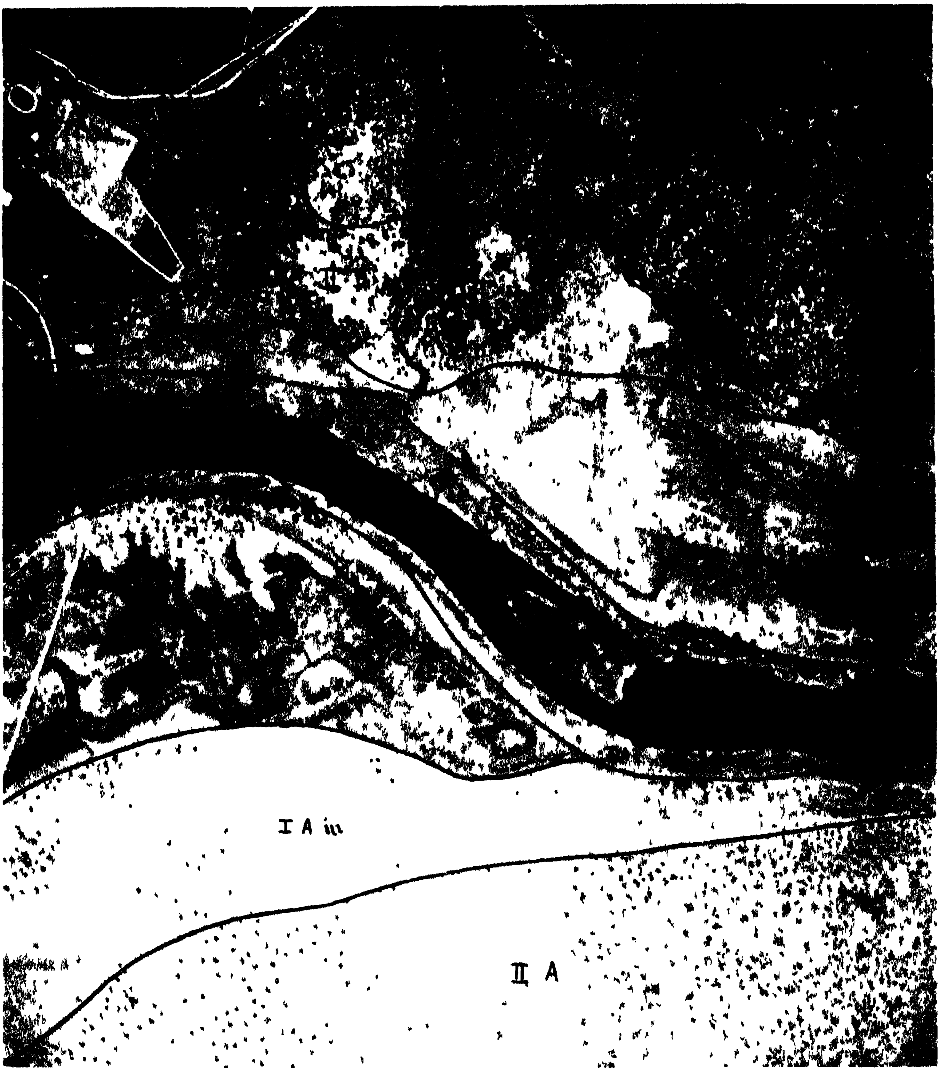
The tree species most typical of all these colluvial lands with adequate water are the figs and the thorns.

Mr C. G. Trapnell notes: "There is no need for this to be treated as an artificial type. It is simply thorn country on fertile colluvial soil in which *Acacia woodii* is dominant, replaced on slight slopes of moist soil by *A. campylacantha*, and in small valleys by *A. hebecladoides*. *Lonchocarpus capassa*, *Bauhinia thonningii* and a characteristic ground flora are associated, with many figs where there is subsoil moisture."

APPENDIX II.

LIST OF SPECIES.

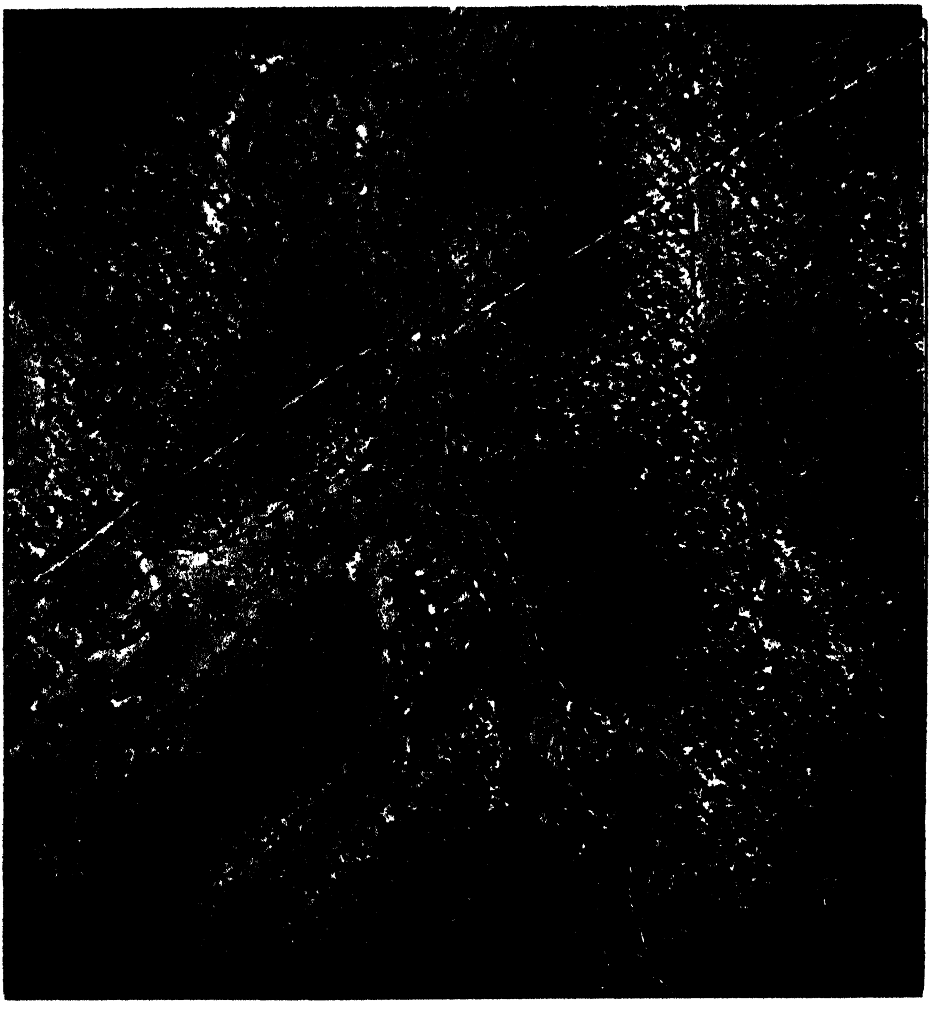
Species	Native name	Type
Acacia arabica	Mukoka	VII, VIII
A. campylacantha	Munga, mutubetube	II, VI, VII, VIII
A. pallens	Mutantasokwe	V
A. seyal	Muski-balosh	VII
A. woodii	Mukoka	VI, VII, VIII
Acacia sp.	Mungoshiya	I
Adansonia digitata	Mu-uyu (baobab)	I, VIII
Afrormosia angolensis	Mubanga	All
Afzelia quansensis	Mukamba	VI, VII
Albizzia buchananii	Lipunga	VII
A. hypoleuca	Kangalla	VI, VII, VIII
A. versicolor	Mububa	VI, VII, VIII
Albizzia sp.	Muzarazambwe	VII
Bauhinia petersiana	Mupondo	VII, VIII
B. thonningii	Musekeso	VII, VIII
Brachystegia filiformis	Musamba	III, IV, V
B. hockii	Mpansi	III, IV, V
B. mimosaefolia	N'galati	IV
B. tamarindoides	Mutwepa	IV
Burkea africana	?	VI
Cassia spp.	Musokansoka	VI, VII
Combretum splendens	Mulama	All
Combretum sp.	Mukutabulonga	VI, VII
Combretum sp.	Mubimba	II, VI
Commiphora sp.	Mubwabwa	V
Copaifera mopane	Mupane	II
Cassia abbreviata	Mululwe	VI, VII, VIII
Dalbergia elata	Mulyamgombe	VI, VII
Dalbergiella sp.	Mwamba	VI, VII
Dichrostachys sp.	Katenge	VII, VIII
Diospyros mespiliformis	Muchenje	II, VI
Diplorrhynchus mosambicensis	Mutowa	III, IV, V, VI
Dombeya sp.	Mukole	V
Ekebergia sp.	Muposho	I
Erythrina spp.	Mutipwetipwe	VI, VII, VIII
Erythrophloeum africanum	Mukoso	IV, VI
Euphorbia cooperi	Mutundungoma	II
Faurea sp.	Musokoto?	VI
Ficus sycamorus	Mukuyu	II, VI, VII, VIII
Ficus sp.	Mukuyu	II, VI, VII, VIII
Hymenocardia mollis?	Kapempe	VIII
Hyphaene sp.	? Palm	VII, VIII
Isoberlinia globiflora	Kabunga	III, IV
Kigelia pinnata	Muzungula	I
Lonchocarpus capassa	Mukololo	VI, VII, VIII



Photographed by the Aircraft Operating Co. of South Africa

No. 02660. Vertical. I A i. Aquatic and reed growth, always submerged.
I A ii. Grass swamp, submerged every flood season for some months.
I A iii. Submerged at highest floods only.
II A. Mupane forest, mainly *Copaifera mopane* and *Euphorbia cooperi*.
II D. Flat land; not submerged but badly drained. No mopane.
III. Steep shale hills with *Brachystegia*, mainly *B. hockii*.
VII A. Foothill type intermediate between III and II D.

ROBBINS—Northern Rhodesia



Photographed by the Aircraft Operating Co. of South Africa

No. 02219. Vertical.

Pl. no. 02219. 1. Many tree species on red soil over mica-schist: undergrowth of shrubs, creepers, etc. 2. Grass vlei. 3. *Brachystegia* spp. on leached sand over quartzite: grass undergrowth.

ROBBINS—NORTHERN RHODESIA

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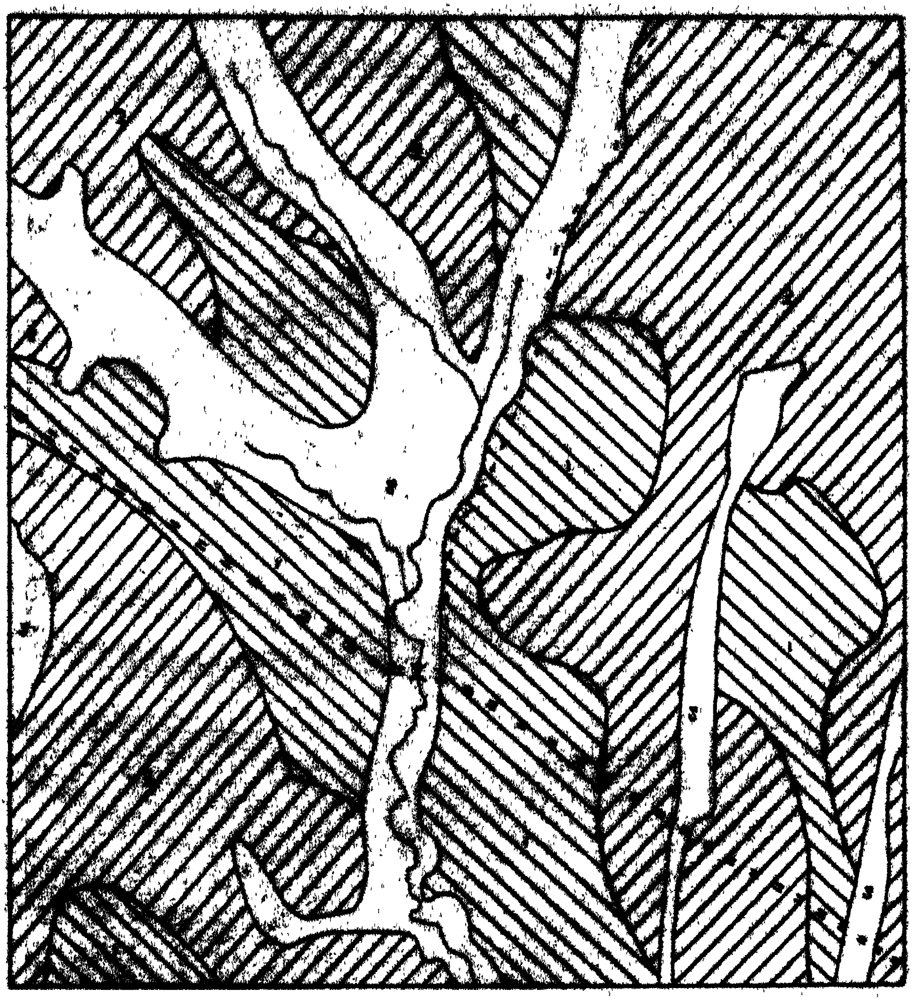
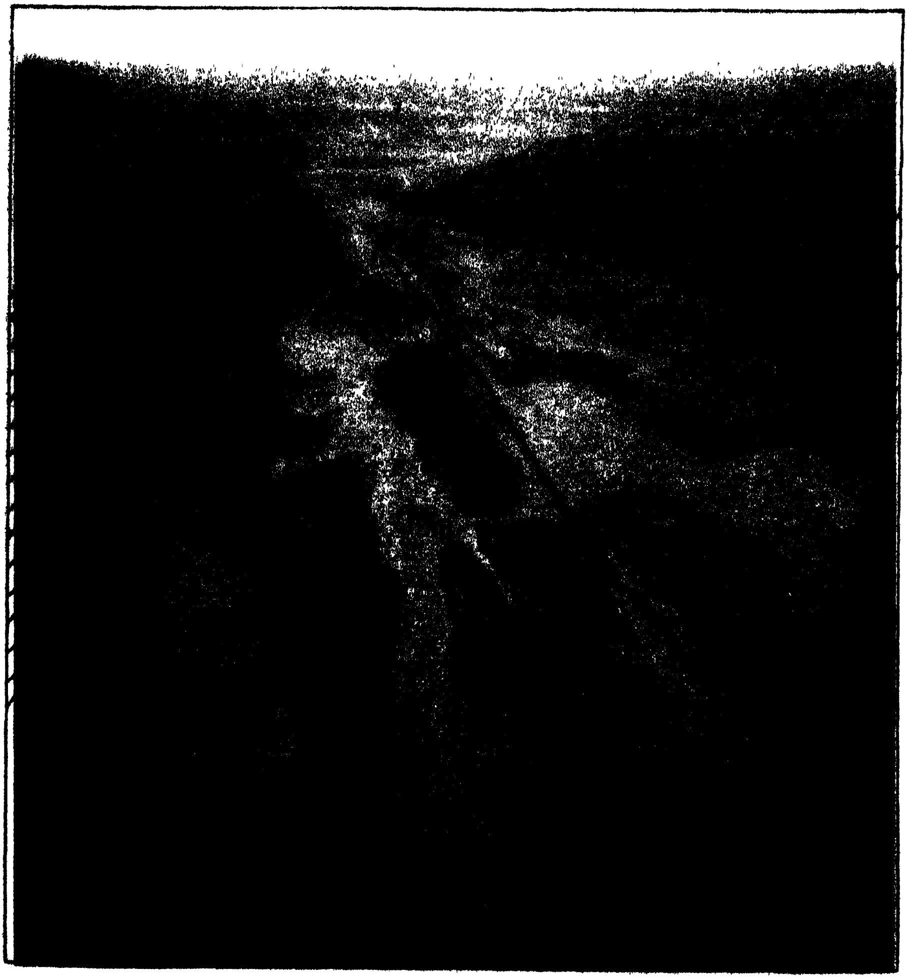


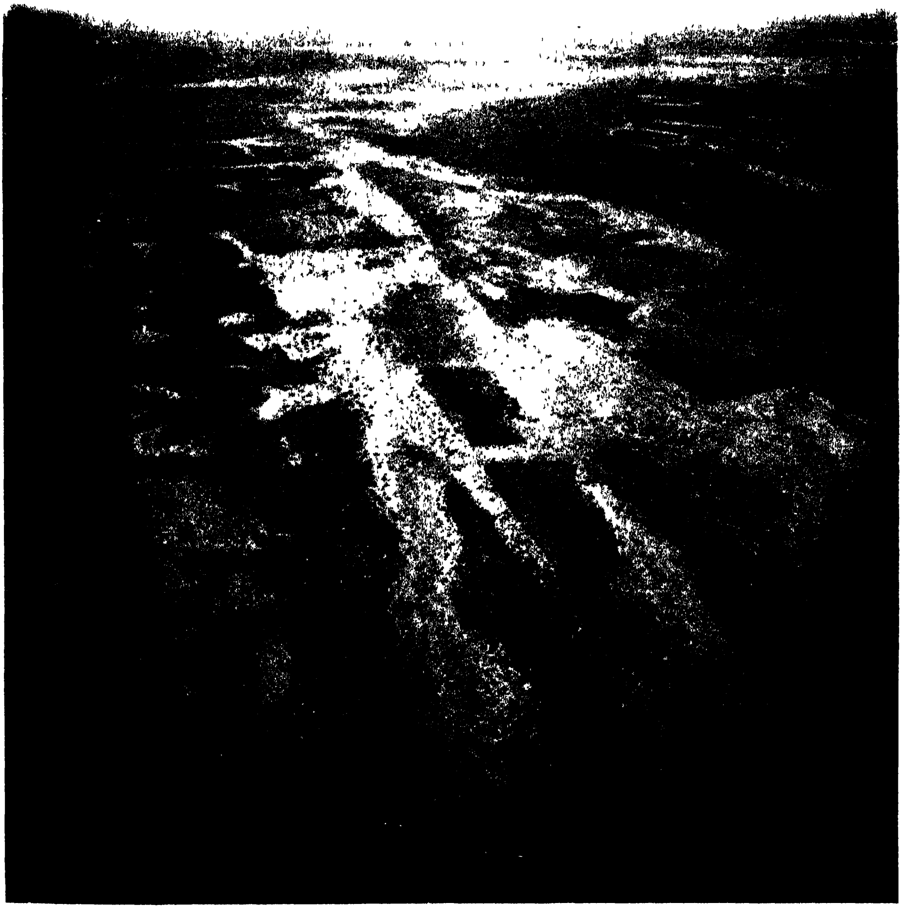


Photographed by the Aircraft Operating Co. of South Africa

No. 02848. Oblique.

Pl. no. 02848. 1. **Mixed schists and quartzites.** 2. Scrub *Brachystegia* spp. and *Uapaca* spp. **on leached sand.** 3. Grass vlei on white sand. 4. Grass vlei on black clay 5. ***Acacia campylacantha*** **on black soil.** 6. *Acacia* spp., *Albizzia* spp. on deep soil over schist. 7. Farms **with cleared lands.**

ROBBINS—NORTHERN RHODESIA

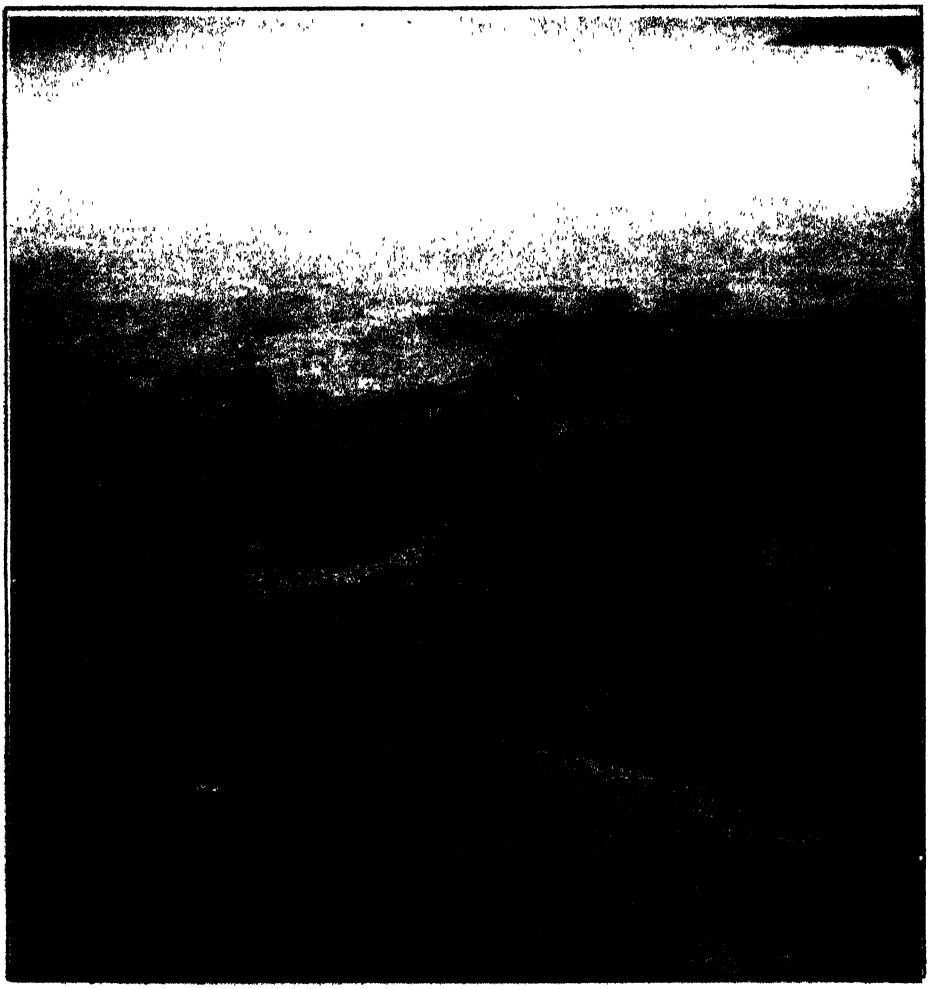


Photographed by the Aircraft Operating Co. of South Africa

No. 02848. Oblique.

ROBBINS—NORTHERN RHODESIA

Face p. 104

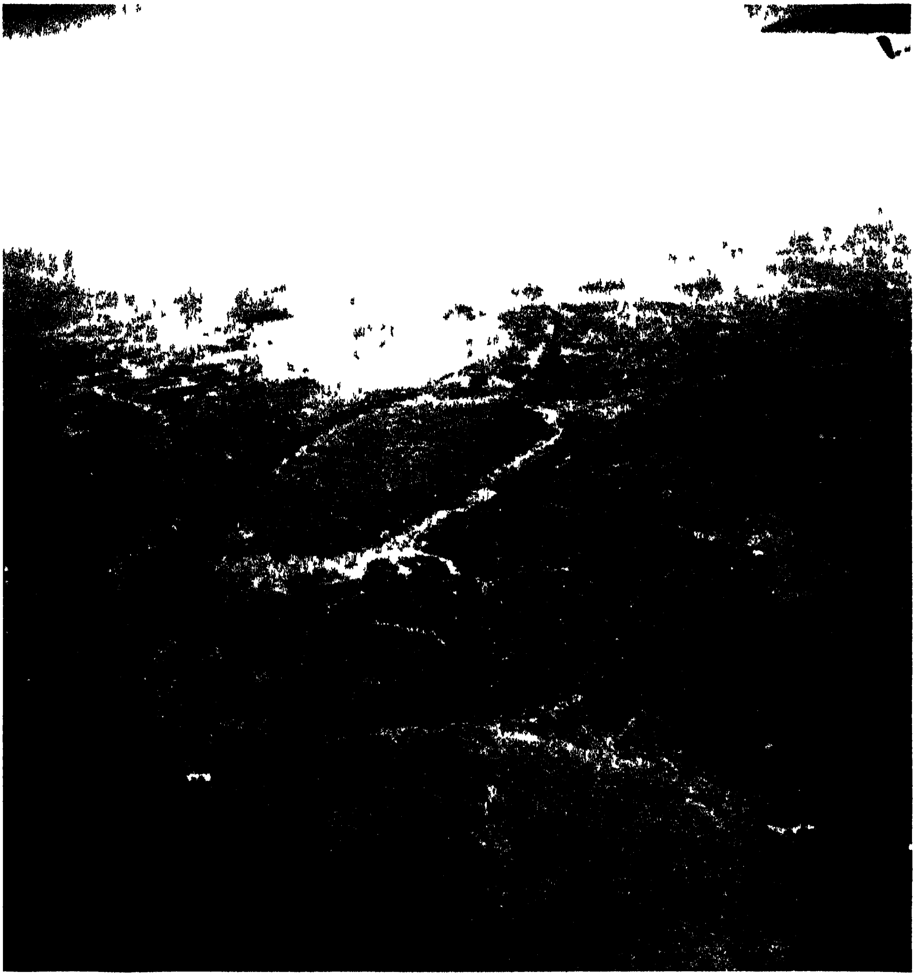


Photographed by the Aircraft Operating Co. of South Africa

No. 02528. Oblique.

Pl. no. 02528. 1. Sandstone-quartzite hills. 2. Flat limestone beds: (1) with trees; medium soil; (2) much outcrop; grass; (3) much cut; deeper red soil. 3. Alluvium. *Brachystegia* spp. dominant on all sites but soil and rock indicated by cutting and conformation.

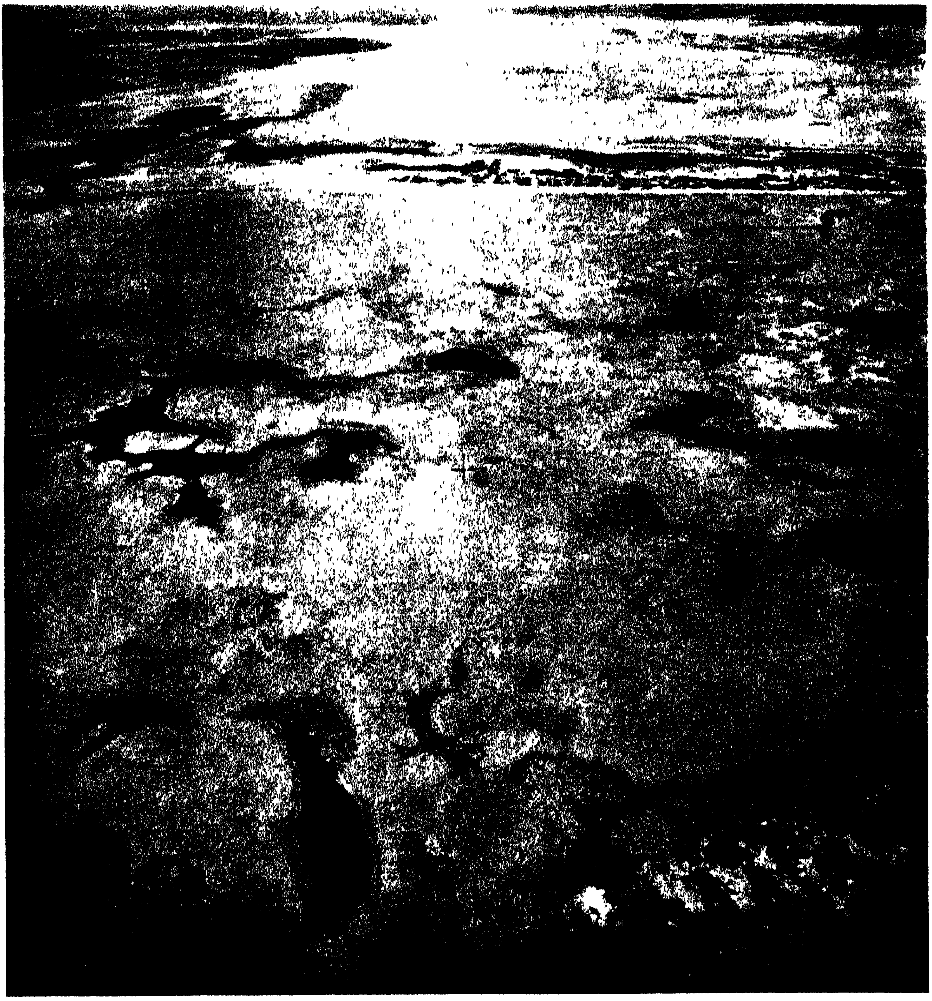
ROBBINS—NORTHERN RHODESIA



Photograph by the Aircraft Operating Co. of South Africa

No 02528 Oblique

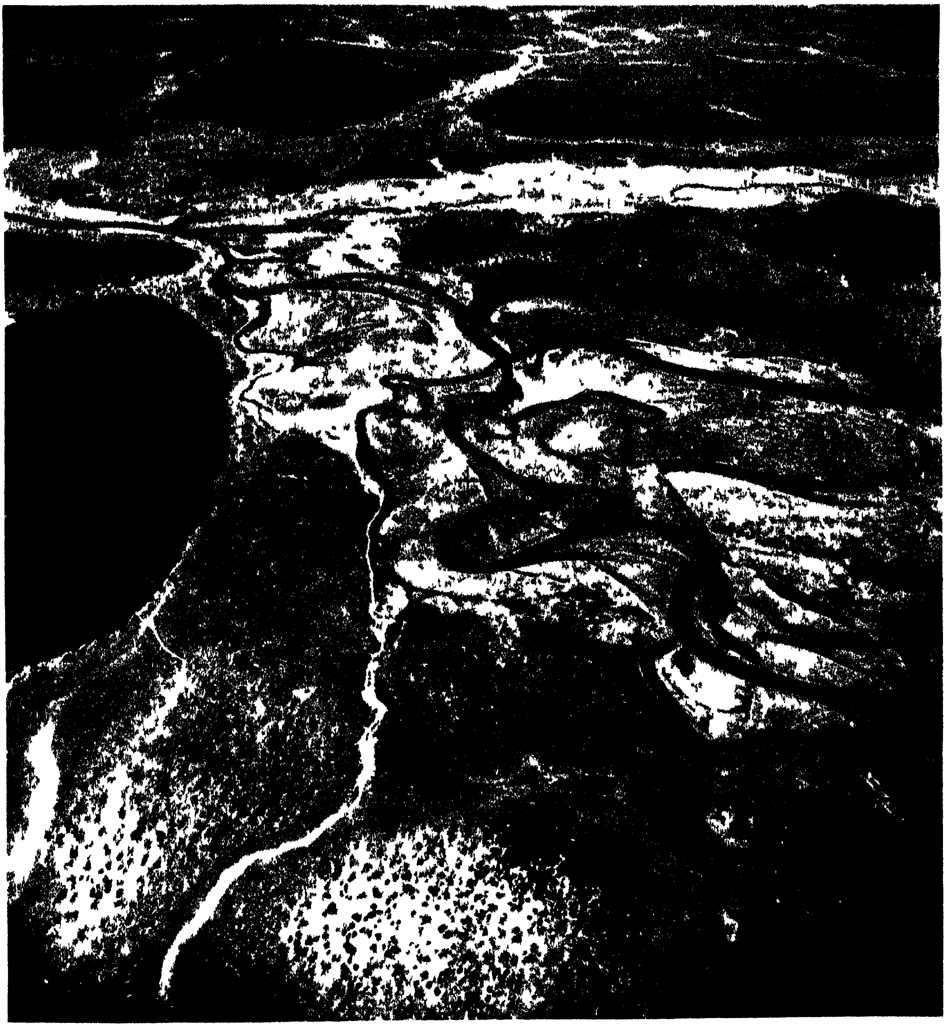
ROBBINS—Northern Rhodesia



Photographed by the Aircraft Operating Co. of South Africa

No. 06548. Oblique (taken outside area surveyed). Part of Lukanga swamp Bush and grassland in distance. Light parts mainly papyrus. Dark patches deep pools of clear water.

ROBBINS—NORTHERN RHODESIA



Photograph by the Aircraft Operating Co. of South Africa

No 06150 Oblique (taken outside area surveyed) showing junction of rivers with changing beds

ROBBINS NORTHERN RHODESIA

LIST OF SPECIES (*cont.*).

Species	Native name	Type
Monotes spp.	Chimpampa	III
Ochna sp.	Musengu	VI, VII
Parinarium mobola	Mubula	IV, VI, VII
Protea spp.	Mushogataw	III, IV, V, VII
Protorhus sp.	Musombo	I, II, V
Pseudolachnostylis glauca	Mukunku	IV, V, VI, VII
Pterocarpus angolensis	Musomaraw	IV, V, VI, VII
Schrebera sp.	Mulyambaso	II
Securidaca longipedunculata	Mufufuma (violet tree)	VII, VIII
Sterculia sp.	Chikatawse	V
Strychnos spp.	Munzhimbilili	V, VI, VII
Syzygium sp.	Mutokolo	I
Terminalia sericea	Kalunguti	VI, VII
T. torulosa	Chibubu	V, VI, VII, VIII
Terminalia sp.	Kafulanjula (Mutwamaila)	VI, VII, VIII
Trichelia emetica	Musikili	I, VI, VII
Uapaca kirkiana	Musuku	III, IV
U. nitida	Mulundu, inundu	III, IV
Uapaca sp.	Musokolowe	IV
Vitex sp.	Mufutu	VII
Zizyphus jujuba	Mukona	VII, VIII

THE VEGETATION OF MORABALLI CREEK, BRITISH GUIANA: AN ECOLOGICAL STUDY OF A LIMITED AREA OF TROPICAL RAIN FOREST. PART II[1]

By T. A. W. DAVIS, B.A. and P. W. RICHARDS, B.A.

(*With Plates XII–XIV and two Figures in the Text.*)

CONTENTS.

	PAGE
I. The synecology of the forest	106
(1) Methods	107
(2) Description of forest types	109
(*a*) Mora consociation	109
(*b*) Morabukea consociation	113
(*c*) Mixed forest association	117
(*d*) Greenheart consociation	120
(*e*) Wallaba consociation	122
(3) Buttressing of trees	126
(4) Comparison of types and discussion	129
II. Summary	132
References	133

I. The synecology of the forest.

The general impression is given in much of the literature that the rain forest formation is exceedingly uniform over very large areas. In British Guiana, at least, this is far from being true. The forest can be divided into a number of distinct types as widely different as the oak and beech woodlands of Western Europe. When the forest is seen for the first time it seems homogeneous, but merely because the only available characters for recognising the species of the canopy trees are those given by the buttresses and bark, and it needs several weeks' experience before they can be appreciated.

Owing to the short time available, only primary (i.e. belonging to the prisere) forest was studied: the subseres caused by burning, clear and partial felling had to be neglected, in spite of their great interest. It was therefore of importance to be able to distinguish secondary (subseral) from primary types. The earlier stages of the subseres are easily recognisable and it was only the later stages which could be mistaken for true primary forest. Large parts of our area were covered with a low, tangled, very mixed type of forest known locally as "Low Bush" which was apparently such a late stage. It occurred on all soils except the driest and the wettest. Though all of it showed evident signs of interference, it might possibly be a peculiar type of primary forest determined by special conditions. According to the previous observations of Davis old secondary forest can be recognised by: (i) the absence of very large hardwood trees, (ii) the high proportion of light-wood (i.e. probably fast growing) species, (iii) unusual abundance of bush-ropes[1], and (iv) the abundance of certain indicators, e.g. *Byrsonima altissima* (Aubl.), *B. rugosa* Benth. and certain species of *Inga*. Abundance of Kabukalli, *Goupia glabra* Aubl., is probably an indicator of former Indian cultivation, though the mere occurrence of the tree is not. According to these four criteria all the "Low Bush" of our area must be considered old secondary forest[2], but it is clear that it will not be possible always to recognise old secondary forest with certainty until the whole secondary succession has been thoroughly studied. As will be seen later (cf. p. 132), the results of the work on the types considered primary, however, give strong confirmation to the view that most "Low Bush" is really secondary.

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[1] Part I appeared in this Journ. 21, No. 2, August, 1933.

Previous workers on the forests of the colony have recognised four types of primary forest in the near interior, viz. Mora, Greenheart, Miscellaneous and Wallaba (2). On the basis of our observations and of Davis' previous experience we recognise five types in our area, viz. Mora, Morabukea, Mixed, Greenheart, Wallaba. Morabukea is an easily recognisable and very distinct type. Previous workers seem to have confused it either with Mora, through not recognising the specific distinctness of Mora and Morabukea, or to have regarded it merely as a special facies of the "Miscellaneous" type. Our "Mixed" type is distinguished from all the others in that it has no single clearly dominant species. Though it is fairly homogeneous, it is certain that if it were carefully studied over a wide area several facies could be distinguished in it.

(1) *Methods.*

The floristic composition of the forest types was worked out by taking a sample plot of each (time did not allow more than one). A piece of forest representative of its type and showing as few signs of previous interference as possible was chosen for each plot. The size of the plots was 400 ft. (122 m.) square (=about 1·5 hectares); this proved satisfactory except for the Greenheart type, which always occurred in narrow curved strips less than 400 ft. wide. In this case two adjacent narrow plots, together equal in area to one of the large plots, were taken.

Each plot was marked out with posts and measured ropes with the help of a prismatic compass. A path through the undergrowth was cut with cutlasses all round the outside of the plot, also a series of paths parallel to one of the sides at intervals of roughly 25 ft. (7·6 m.), dividing the plot into a number of narrow strips. Trees over 4 in. (10 cm.) in diameter at breast height were counted over the whole plot, strip by strip. Trees under 4 in. in diameter and over 15 ft. (4·6 m.) high were counted only on two narrow strips exactly 25 ft. (7·6 m.) wide taken across the whole width of the plot. Each tree had its native name given and its diameter class[1] estimated by an Indian assistant, who blazed each tree with a cutlass as soon as it was recorded in the notebook.

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[1] In one type of Low Bush, the "*Mibiokilli*" of the Indians, they are so abundant as to make the forest almost impenetrable. This is probably a fairly early stage in the subsere.

[2] Wood states (1) that in the Bartica-Kaburi area "Low Bush" occurs near creeks, which show distinct signs of having been cleared of fallen logs to allow navigation, and not elsewhere.

This Indian had had much experience in identifying and counting trees on the valuation surveys of the Forestry Department of the Colony and had been found to be exceptionally reliable. The Arawaks have several hundred native names for trees and many other (mainly useful) plants. They identify trees entirely on the characters of the trunk, viz. shape and nature of buttresses (if any), character of bark, especially as shown by the blaze, colour of latex (if any), smell, colour, structure and texture of wood. The comparatively few species of trees which are identical in all these respects they refuse to recognise as different, however distinct they may be in flowers and leaves (e.g. "Ituri Wallaba" includes three species, *Eperua Jenmani* Oliv., *E. grandiflora* (Aubl.) and *E. Schomburgkiana* Bth., which are identical in trunk characters, but entirely different in the flowers). The reliability of the names used by our Indian was tested very carefully. Several individuals of trees to which he gave the same name were cut down and specimens collected. Others were examined from below with field-glasses. It was found that the native names in a few cases included a large number of different species within a single family (e.g. "Awassakuli," which means various superficially similar species of *Clusia* and *Tovomita*), "Kokeritiballi" = various Sapotaceae. The only names found to include members of more than one family were Kulashiri (Meliaceae, Flacourtiaceae and Sapindaceae), and Mabwa (*Sapium* sp. and *Plumeria* sp.). Fairly frequently they included two (e.g. "Baromalli" = *Catostemma fragrans* Bth. and *C. commune* Sandwith) or a large number of species (e.g. "Warakusa" = *Inga* spp., excluding certain easily recognised species) in one genus. In the great majority of cases, however, we found that each Indian name corresponded to one species only. Sometimes the Indians are even "Splitters" (thus they recognise three kinds of Greenheart, which cannot be called even varieties in the herbarium). A striking instance of the acuteness of observation of the Indians is the case of the Fine-leaved and Large-leaved Yarri-yarris, which they recognise as different, though in the field we were unwilling to admit them as distinct species. Later, however, in the herbarium they proved to be such (*Duguetia neglecta* Sandwith and *D. pycnastera* Sandwith). Our collections are sufficient to allow us to identify a large proportion of the native names of the trees found on our plots and to decide whether they correspond to one, two or several species. In some cases where a name includes two or three very distinct species it was possible to tell in the field to which the name was being given.

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[1] All diameters of trees given in this paper refer to the diameter at breast height or above the buttresses.

It is clear that while enumeration by native names is not a rigidly accurate nor absolutely satisfactory method of working out the floristic composition of a tropical forest, at least it is the only one at present available and does give very useful results[1]. The theoretically sounder method of cutting down and collecting herbarium material from all the trees on a plot would probably give hardly better results, since only a small proportion of the trees would ever be in flower together and identification by leaves is not likely to be much more accurate than that based on trunk and bark characters alone.

The smaller undergrowth and the ground flora of the plots were enumerated by the ordinary method of listing. The only synusia which had to be neglected altogether were those of the epiphytes and of the larger creepers. There are many native names for the large bush-ropes, but it is extremely difficult to correlate bark and other characters for not only is it not easy to decide exactly on which tree a particular rope is growing, but each tree will often have so many different ropes that it is a slow and troublesome business to discover which flowers belong to which rope.

General observations were made on each plot, as well as measurements of light intensity near the ground. A pit was dug in each to show the soil profile and soil samples were taken for analysis.

(2) *Description of forest types.*

(*a*) *Mora consociation.*

The Mora forest has a characteristic appearance which makes it easily recognisable. The dominant tree, *Mora excelsa* Bth., is of enormous size; mature specimens average over 30 m. in height and specimens of 40 m. are common. The huge plank-buttresses of this species are one of the chief features of this type of forest. On mature trees they usually reach to a height of over 6 m. and spread out from the base for about an equal distance. A considerable number of the subsidiary tree species are also strongly buttressed. Mora is a comparatively well-illuminated type of forest[2], and the abundance of ground herbs, of mosses and other epiphytes at low levels is striking. In spite of the comparative openness of the canopy, the atmosphere in the undergrowth is always nearly saturated and feels very oppressive (Part I, Table VI). This characteristic is reflected by the abundance of foliose liverworts and filmy ferns on the branches of the smaller trees and the covering of epiphyllae on all the older leaves in the undergrowth.

The Mora forest occupies the lowest ground. It forms a broad strip along both banks of Moraballi Creek (and along the Essequibo where it has not been cleared) and narrower strips follow the larger branch creeks. Most of it is liable to flooding for a long period during the long wet season and occasionally for a few days at a time in the long dry season. During the dry seasons the level of the creek falls to at least 2 m. below its normal level at the end of the wet seasons, but the water-level in the soil sample pit in the Mora plot was only 46 cm. below the surface even at the height of the long dry season. There were a few places where the Mora forest was not confined to the flood plain and extended over a limited area some way up the hill sides. In every case this occurred on steep rocky slopes where the ground was strewn with boulders and the soil apparently extremely shallow. It seems as if this forest type is determined by shallowness of soil, whether produced by rockiness or by a high water-level. The total number of trees over 16 in. (41 cm.) diameter on the plot is considerably smaller than in any other type of forest.

---

[1] Judging from the literature Guiana is exceptionally favoured in the number and precision of the native names.

[2] This is not always true in other parts of the colony. For instance, in the very fine Mora forests of the Cuyuni River the illumination is about as low as in the Morabukea forests of Moraballi Creek, according to the recent observations of Mr G. S. Carter.

The soil in the sample pit was a fine, sticky, dirty white silt. A dull brown layer of dead leaves, about 2 cm. thick[1], covers the surface, except near the creek banks, where the current of flood water is strong enough to wash it away. Below this there is a layer of silt 15 cm. thick, tinged slightly brown with humus (not a measurable amount). Beneath this the whitish silt continues down to the water-level.

The soil samples gave the following results:

Depth cm.	*p*H	Comber colour	KCl *p*H	Moisture at point of stickiness* %	% of sand (1·0–0·04 mm.)*	% of gravel (over 1 mm.)*	Index of texture	Organic matter content %
0–15	4·75	Light red	4·23	40·5	26·3	0	35 (fine silt)	0·81
15–45	4·85	Red	4·23	47·5	36·5	0	40 (fine silt)	—

* The *p*H was determined by the quinhydrone electrode method, the organic matter content by a wet combustion method. For the significance of the "Moisture at point of stickiness" and the "Index of texture," see the paper by **Hardy** (**3**).

On large patches mostly near the creek bank this heavy soil was overlaid by a layer of fine, whitish sand about 30 cm. deep. The soil of the Mora forest on rocky slopes was very heavy and sticky, but was not closely examined.

On the sample plot *Mora excelsa* forms 67·2 per cent. of all trees over 16 in. (41 cm.) diameter, but only 23·4 per cent. of all trees over 4 in. (10 cm.) diameter. The percentages in the separate size classes are as follows:

4–8 in. (10–20 cm.)	8–12 in. (20–31 cm.)	12–16 in. (31–41 cm.)	16–24 in. (41–61 cm.)	Over 24 in. (61 cm.)
13·6 %	13·5 %	35·4 %	54·6 %	91·3 %

Regeneration is abundant, though the abundance is much less than that of Morabukea in Morabukea forest. Counts on six separate square metres taken at random over the drier parts of the plot gave an average of 2·7 seedlings under 3 ft. (0·92 m.) high per square yard and two of 3–6 ft. (0·92–1·83 m.).

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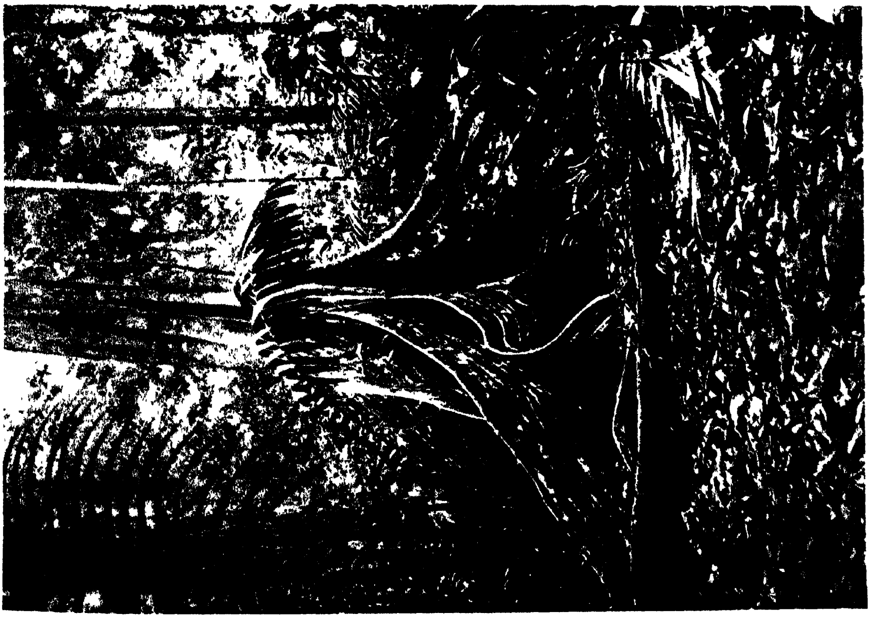
[1] The leaf litter and humus layers are nearly always remarkably thin in the Guiana forest, doubtless owing to the rapid rate of decay.

Phot. J. E. Duffield

Phot. 1 (left). An average sized mature tree of *Mora excelsa* Bth.

Phot. 2 (above). Herbaceous undergrowth in well-illuminated Mora forest. *Rapatea paludosa* Aubl., *Carludovica* sp. (a large plant near centre of picture), *Monotagma Parkeri* (Roscoe) (leaf with prominent ribs in middle of foreground); young palms in the background.



Phot. R. W. G. Hingston

In the damper hollows the number is much less than one per square yard. These numbers are probably about representative for the Mora forests of our area, though in Mora forest at Akaio Landing on the Cuyuni River the seedlings formed a dense thicket like those of Morabukea. Mora is found as isolated and usually very large solitary individuals in all the other types of forest except Wallaba: such isolated individuals in Mixed forest were often surrounded by a denser thicket of seedlings than was ever seen in the Mora forest itself. These facts seem to suggest that the optimum conditions for the species, at any rate in the seedling stage, are not those under which it becomes dominant. It may be that it is dominant on water-logged and shallow soils, not because it prefers them, but because it is not as adversely affected by them as are the species with which it has to compete on the drier and deeper soils.

The subdominant trees are *Pterocarpus officinalis* Jacq. (Corkwood), 10·2 per cent. above 4 in. diameter, 6·0 per cent. over 16 in.; *Pentaclethra macroloba* (Willd.), 10·2 per cent. over 4 in., 3·8 per cent. over 16 in., and *Aldina insignis* (Bth.) (Dakamaballi), 5·8 and 7·5 per cent. The last species was far more abundant in the sample plot than in the Mora forest generally.

Only a few of the subsidiary tree species are confined to the Mora consociation, e.g. *Eperua Schomburgkiana* Bth., *Macrolobium bifolium* (Aubl.); many range through all the four other types, though a fair proportion is not found in the Wallaba type. There were only about fifty-six tree species besides the dominants and subdominants on the sample plot, a smaller number than in any of the other plots.

It is a striking fact that the dominant and the subdominants are all members of the Leguminosae. This family forms about 59 per cent.[1] of all trees (individuals) over 4 in. diameter.

One species of palm, Manicole, *Euterpe edulis* Mart. (?), is fairly frequent, but typically there are few palms in well-developed Mora forest.

The canopy is fairly open and does not cast a very dense shade. Two readings of the illumination[2] at breast height gave a mean of 1/75 of that in the open, which is about twice that in Morabukea, the shadiest type of forest. With such good illumination it is to be expected that the undergrowth layers should be comparatively well developed.

The majority of the trees in the undergrowth layer consists of young individuals of the dominant and subdominant, but though the total bulk of this stratum is less than in the Morabukea type the abundance of true undergrowth species is greater. Annonaceae are by far the most numerous family among the latter: the most abundant species is Kurihikoyoko, *Anaxagorea dolichocarpa* Sprague et Sandwith, which forms 11·2 per cent. of all trees over 15 ft. (4·6 m.) in height and under 4 in. (10 cm.) diameter.

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[1] The figures for the percentage of Leguminosae are only approximate, as some of the trees whose flowers were not seen cannot be certainly assigned to their family. Very abundant nodules (presumably bacterial) were noticed on Mora roots.

[2] All light intensity measurements were made with an "Imperial" exposure meter. The observer walked about continually during the exposure to get a rough average of the illumination in sun flecks and deep shade. The illumination in our large camp clearing was taken as equal to that in the open.

A characteristic feature of Mora forest is the luxuriance and density of the tall herb layer. There are, however, large patches where ground herbs are as scarce as in the "central" types of forest. The bulk of both herb layers is made up of herbaceous plants, as small tree seedlings are relatively uncommon. Social herbs forming large conspicuous colonies are *Monotagma Parkeri* (Roscoe), *Rapatea paludosa* Aubl., *Carludovica* sp. and the grass, *Pariana radiciflora* Sagot ex Doell.—all monocotyledons. The first species often forms patches of closed vegetation many square metres in extent. The first two species are most abundant on the patches of sandy surface soil referred to above. The herb layers may be divided into two societies of widely different floristic composition, that of the swampy hollows with *Carludovica* sp. as the most abundant species and that of the drier ground with no *Carludovica*. The swamp society consists mainly of tall herbs; the latter includes many species of small herbs, including a fair number of ferns. Saprophytes are very scarce, but six species were collected, one of which (*Campylosiphon purpurascens* Bth.) was seen in no other type of forest.

The herbaceous ground flora of the Mora forest is much richer in species, as well as in individuals, than that of any other type. A large number of species including the fairly abundant social species are confined, or nearly so, to this one type of forest. Of the rest, the majority occur in all the other types or all except the Wallaba type, but one very interesting group occurs in Mora and Wallaba only, missing out the three "central" types (cf. p. 125).

Bush-ropes of the canopy are rather less abundant in the Mora forest than usual. Very few seem to be confined to this type (an example is perhaps *Markea porphyrobaphes* Sandwith).

The great abundance of epiphytes and the low level to which they descend has been described above (Part I, p. 382). The community of shade epiphytes is particularly well developed in the swampier parts of the Mora forest.

The Mora forest bordering the creek has some important differences from that farther away from the water; climbers, epiphytes and ground herbs are all very much more abundant than elsewhere. On the inner side of bends in the creek and in other places where the bank slopes down comparatively gently to the water, there is a characteristic fringing vegetation growing in the shallow water, consisting mainly of four species, *Pithecellobium adiantifolium* (H.B.K.), (Immirimia), a tall shrub; *Montrichardia aculeata* Crug. Mukka-Mukka, an aroid averaging 4 m., but sometimes reaching 6 m., in height, *Carludovica* sp. (the same species as in the interior of the Mora forest), and *Dieffenbachia paludicola* N.E. Br., the last two being tall herbs 1–1·5 m. high. Along great stretches of the creek bank the last two species only are found, the first two growing only in the better lit places. A large number of species of scramblers and small climbers were never seen except on the creek bank.

On very swampy ground a special facies of Mora forest is found in which palms are very abundant (*Euterpe edulis* Mart., *Maximiliana regia* Mart., *Mauritia flexuosa* L., *Jessenia oligocarpa* Griseb. et H. Wendl. Large societies of *Heliconia Bihai* L. are a striking feature. This type was more open and brightly illuminated than the typical Mora forest and the dry society of the ground flora was lacking, but otherwise it did not differ much from the normal type. It is probably an approach to the "Swamp Savannah" of the coastal region in which palms are dominant.

Another special facies was found on the small areas where the clay soil was overlain by sand. This was characterised by the abundance of *Aldina insignis* (Bth.) (Dakamaballi), and Soft Wallaba, *Eperua falcata* Aubl. Nearly all the characteristic undergrowth species of the Wallaba consociation occur in this facies (only a few of them occur in typical Mora forest). The characteristic subdominant tree species of the Wallaba forest, *Catostemma fragrans* Bth. and *Licania buxifolia* Sandwith are, however, entirely lacking. About a third or a quarter of our sample plot belonged to this facies.

The facies of Mora forest on rocky hill slopes was not closely studied, but general observations showed that the undergrowth was very similar to that of Mixed forest on the same kind of ground. The great abundance of ferns and the presence of species confined to these steep rocky slopes (e.g. *Adiantum olivaceum* Bak. and *A. phyllitides* J.Sm.) is noticeable. This facies has a closed canopy and illumination is about as low as in the "central" types of forest.

The Mora forest type has a wide distribution in British Guiana near the coast and ascends the river valleys to above the first falls. It is particularly finely and extensively developed in the low-lying North-West District. It occurs in Surinam, in the Orinoco delta region and formerly covered large areas in the central plain of Trinidad (though it is now represented there only by comparatively small relics).

(*b*) *Morabukea consociation.*

This type of forest, dominated by another species of *Mora, M. Gonggrijpii* (Kleinhoonte) has an entirely different general appearance from that of the true Mora forest. The Morabukea tree is smaller on the average than *Mora excelsa*, though occasional specimens are as tall as the largest Moras. Morabukea is also a strongly plank-buttressed tree, but the buttresses seldom reach more than 2–3 m. above the ground. Morabukea is much the darkest type of forest, and the deep gloom is one of its most striking features. Another very conspicuous characteristic is the dense thicket of seedlings of the dominant species, all about 1–1·5 m. high, which is usually present. Epiphytes seem to be quite absent, and the herbaceous ground flora, as might be expected, is very sparse. In this respect, as well as in the dense reddish brown carpet of dead leaves, the Morabukea forest is reminiscent of an English beech wood.

Morabukea forest is never found on flood plains: it is found on the lower slopes of the smaller, flat-topped hills (mostly under 50 m. high) and may extend over their summits if the soil is suitable. It only reaches the creek bank where the ground is high enough to be raised well clear of floods. In general the Morabukea land is damp, but well drained. In our district this consociation was seldom seen covering large tracts without a break, but the total area is considerable.

The soil is typically a very heavy, sticky, bright red clay, which is probably of a lateritic nature[1]. The soil profile on the sample plot showed under the dead-leaf litter, which was about 3 cm. deep on the average, a layer 20 cm. deep tinged grey by humus. The next 45 cm. was yellow-brown with reddish streaks and patches. Below 60 cm. the clay became very hard and whitish streaks appeared. Analysis gave the following results:

Depth cm.	*p*H	Comber colour	KCl *p*H	Moisture at point of sticki-ness %	% of sand (1·0–0·04 mm.)	% gravel (over 1 mm.)	Index of texture	Organic matter content %
0–20	4·63	Red	3·93	48·0	54·9	67·7	37 (fine silt)	4·96
20–65	4·67	Light red	4·38	49·1	28·2	10·0	44 (heavy silt)	—
66–90	4·82	Pale pink	4·35	53·5	35·3	0	46 (clay)	—

The organic matter content in this topsoil is by far the highest observed in any of our samples. It is doubtless due to the unusually thick layer of dead-leaf litter. This sample is probably representative of the Morabukea consociation as a whole, but patches of it were occasionally met with on much lighter soils, some being loamy and some almost sandy, at least in the top few centimetres. It seems, however, that it is the resultant effect of soil texture physiognomic features which determines the forest type. Thus these patches of the Morabukea forest on lighter soils were invariably situated on low-lying ground at the foot of hill slopes[2]. In our area the Mixed type of forest occupies as a rule higher ground than the Morabukea type and prefers lighter soils, but it may happen that the Morabukea forest occupies the flat top of a hill and the Mixed forest the steep sides. This is no doubt due to the fact that the soil on the steep sides is lighter, having had much of its finer fractions

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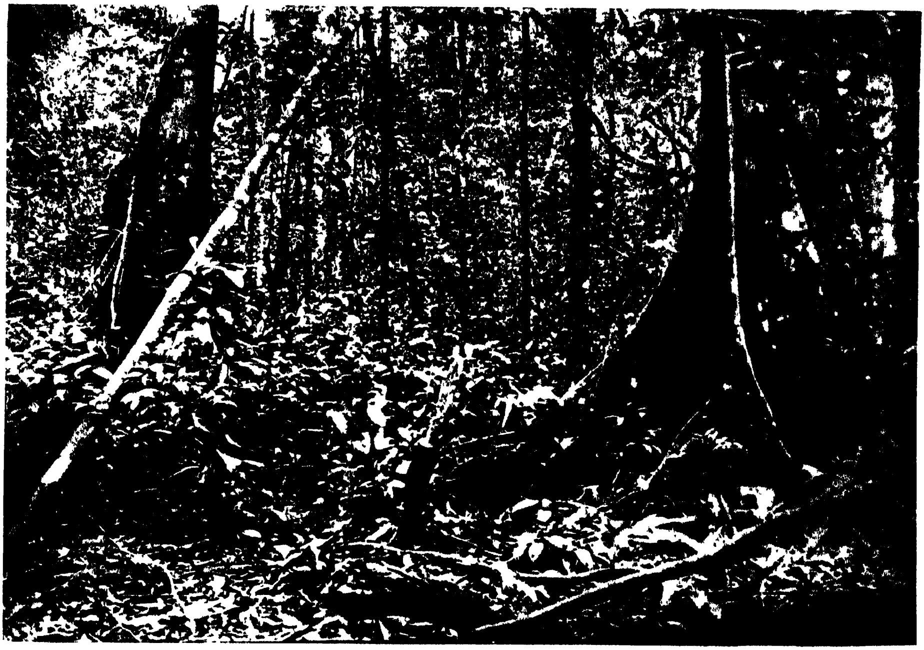
[1] Mr Follett-Smith reports that "it has not been possible to determine the silica-alumina ratio in these soils and it is impossible to state definitely whether they are lateritic. It is probable, however, that they are of a lateritic nature."

[2] In some parts of the colony Morabukea forest is found on red sandy soil on hill saddles: it was in such situations that the heavy mortality among seedlings, apparently due to drought, was observed in 1925–6 (cf. Part I, p. 356).



Phot. R. W. G. Hingston

Phot. 3. Morabukea Forest Showing two large trees of the dominant (*Mora Gonggrijpii* [Kleinh.]). Seedlings are less abundant than usual in this type of forest.

Phot. J. F. Duffield

Phot. 4. Wallaba Forest (dominant *Eperua falcata* Aubl.). Two trees of *Eperua* sp. in the middle of the picture: note absence of buttresses. The grass-like plants to the left of nearer *Eperua* are *Tillandsia* sp. which have fallen from the tree tops and taken root in the ground. Another *Tillandsia* can be seen growing only a few feet above ground level on the small tree to the left.

washed out: thus difference in soil texture here reverses the usual relative position of the two forest types.

The dominance of Morabukea seems more complete than it really is, owing to the extremely abundant regeneration. On the plot Morabukea formed 60·7 per cent. of all trees over 16 in. (41 cm.) and 25·9 per cent. of trees over 4 in. (10 cm.) diameter. In the separate size classes the percentages are:

4–8 in. (10–20 cm.)	8–12 in. (20–31 cm.)	12–16 in. (31–41 cm.)	16–24 in. (41–61 cm.)	24 in. (61 cm.) and over
17·6 %	16·5 %	19·6 %	61·3 %	59·3 %

The extraordinarily abundant regeneration, which has already been noticed, is characteristic of the species whether in its own consociation or in other forest types. Counts on six square metres in different parts of the plot gave an average of 11·7 seedlings under 6 ft. (1·83 m.) high per square metre. The height of these seedlings is extraordinarily even (about 1·5 m.)[1]. Occasional patches are found however in which there are no seedlings.

The subdominant species are:

	% of all trees over 4 in. (10 cm.) diam.	% of all trees over 16 in. (41 cm.)
Eschweilera Sagotiana Miers (Common Black Kakaralli)	7·4	5·6
Catostemma commune Sandwith (Baromalli)	5·0	2·2
Pentaclethra macroloba (Willd.) (Trysil)	4·6	1·1
Ocotea Rodioei (Schomb.) (Greenheart)	3·9	9·0
Licania venosa Rusby (Kautaballi)	3·5	2·2

Only one of these is leguminous. Leguminosae form about 33 per cent. of all trees over 4 in. diameter.

There were about sixty-five subsidiary tree species over 4 in. (10 cm.) diameter on the plot.

The deep shade which is a conspicuous difference from the Mora forest is due partly to the greater number of large trees than in the Mora forest (eighty-nine trees over 16 in. diameter on the plot, as against sixty-seven on the Mora plot), to the more compact crown of Morabukea and possibly also to the more even canopy. The average illumination at breast height (two measurements) is 1/163 of that outside, the lowest figure for any of the five forest types. The readings were made above the level of the seedling thicket, so that the average illumination on the ground must be very small indeed, and it is no wonder that the ground vegetation is scanty. The humidity of the atmosphere in the undergrowth is about as high as in the Mora type (see Part I, Table VI).

The layer of undergrowth trees is well developed but has no specially characteristic species, its list of species being very like that of the same layer in the Mixed and Greenheart types of forest. The proportions in which they occur, however, are characteristic of this type. The Annonaceae are scarce and the most abundant species is *Paypayrola longifolia* Tul., a member of the Violaceae. It forms 11·1 per cent. of the trees under 4 in. (10 cm.) diameter and over 15 ft. (4·6 m.) high.

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[1] The apparently even-aged appearance of these seedling thickets may possibly be because the tree only seeds abundantly at intervals of several years: it certainly flowers infrequently.

The herb layers are naturally extremely scanty and represented only by isolated individuals: there is no closed vegetation. The fern and green herb societies are represented by a fair number of species but few individuals, and these are mostly confined to small local well-illuminated patches. The floristic composition of these two societies is very different from that of the Mora consociation, but practically identical with that of the Mixed type.

A characteristic feature of the ground flora is the abundance of saprophytes. This society is here represented by more species and many more individuals than in any other forest type. The saprophytes prefer the deepest shade under the densest seedling thicket; they are not spread evenly through the forest, but occur in colonies a few metres in diameter, usually situated in slight hollows where the thickness of the dead-leaf carpet was above the average. Every colony was formed of several species, and the frequency of the plants in each was about two per square metre on the average. The abundance of the little fern *Schizaea fluminensis* Miers was particularly characteristic, though it occurs sporadically in all the other types of forest.

Bush-ropes are fairly abundant and have a rather marked tendency to form large horizontal loops.

Epiphytes are confined to very high levels, in relation to the low illumination, and are in fact often scarcely noticeable from the ground, except in openings.

A special facies of the Morabukea forest type is found in which the proportion of Greenheart is very much higher than in the sample plot. This was seen in Moraballi Creek, but the conditions which determined it were not studied.

Morabukea, owing to its abundant regeneration, is an aggressive species, and a tendency has been noticed by Wood (**1**, p. 7) for it to replace Greenheart after fires. It is possible therefore that not *all* Morabukea forest is a stable, climax type: there may be two kinds of Morabukea forest, climax and seral. There was no reason for suspecting that the Morabukea forest in the Moraballi area was not a stable climax type.

Morabukea forest has a rather local distribution in the colony. It covers very large areas in parts of the near interior (e.g. the Ebini Hills) and does not reach much nearer the coast than the Moraballi district. In the North-West District Morabukea is rare (**4**, p. 165). It is only known outside the colony from Surinam, where it is said to be fairly abundant. Where the Morabukea type is not found the Mora forests pass above directly into Mixed forest: this may also happen in districts where Morabukea is found.

(c) *Mixed forest association.*

While four of the forest types of our area are exceptional among tropical rain forest communities in having single dominant species there is one type which approaches the more normal condition of no single clear dominant. It is a curious fact that even here a small number of closely allied species of one family are together clearly dominant. This state of affairs is like that in some Philippine forests where members of the Dipterocarpaceae may form up to 31·6 per cent. of all the trees, though no single species forms more than about 16 per cent. (**5**). Owing to the large number of species, none of which is abundant enough to lend the association as a whole a special appearance, it has the varied aspect usually considered characteristic of tropical forests. Trees with large buttresses are relatively uncommon, but there are also few entirely unbuttressed trees. The average height of the trees is probably somewhat less than in Morabukea forest.

This type of forest covers a good deal of the lower hilly land in the Moraballi district. It covers the hill tops when they have no white sand cap and the soil is not very stiff red clay. It prefers a rather sticky yellow-brown loam, intermediate between the heavy clay of the Morabukea forest and the brown sand of the Greenheart forest, but occasionally extends on to lighter or heavier soils. The surface is covered with a layer of dead leaves on the average 1·5 cm. thick. The colour of this layer is a deep dull brown, a tint between the reddish brown of Morabukea and the pale dull brown of Mora. The underlying soil is yellow-brown, the colour being almost uniform to a depth of at least 1 m., though the top 4 or 5 cm. are slightly tinged with humus. The results of analysis were:

Depth cm.	*p*H	Comber colour	KCl *p*H	Moisture at point of stickiness %	% of sand (1·0–0·04 mm.)	% of gravel (over 1 mm.)	Index of texture	Organic matter content %
0–25	4·34	Deep red	4·18	25·6	65·2	6·5	13 (light loam)	1·91
25–60	4·72	Light red	4·28	28·1	52·3	4·1	18 (light loam)	0·91

The most abundant species of canopy trees are:

	% of all trees over 4 in. (10 cm.) diam.	% of all trees over 16 in. (41 cm.) diam.
Pentaclethra macroloba (Willd.) (Trysil)	11·3	6·7
Licania venosa Rusby (Kautaballi)	9·5	11·1
L. laxiflora Fritsch (Kauta)	6·5	6·7
Licania heteromorpha Bth. var. *perplexans* Sandwith (Kairiballi)	6·4	0
Eschweilera Sagotiana Miers (Common Black Kakaralli)	6·1	15·6
Ocotea Rodiaei (Schomb.) (Greenheart)	4·4	14·4

For another tree which was enumerated on the plots as "Smooth-leaved Kakaralli" the percentages were respectively 6·5 and 15·6, but it later proved to be two species which could only be separated when in flower.

There is thus no clear dominant, though four closely allied species of *Eschweilera* together form 17·8 per cent. of all trees over 16 in. in diameter and 12·8 per cent. of those over 4 in. The abundance of the most abundant species in this association is of the same order as that of the subdominant species in the Mora and Morabukea consociations.

Leguminosae form a smaller proportion (15 per cent.) of the total number of trees (over 4 in. diameter) than in any other type of forest except Greenheart.

The Mixed forest association is fairly dark, though not so dark as the Morabukea consociation. The average illumination on the sample plot (two measurements) was 1/150 of that in the open. The humidity of the atmosphere in the undergrowth is distinctly lower than in the Mora and Morabukea types, though much higher than in the Wallaba type (cf. Table VI, Part I).

There are about eighty-five less abundant canopy tree species. The majority of these are the same as in the Morabukea and Greenheart types. A large proportion of all the tree species found in the district may be found in the Mixed type of forest.

Palms are found occasionally in the lower part of the canopy. Turu (*Jessenia oligocarpa* Griseb. et H. Wendl.) is the most abundant species.

The undergrowth tree stratum contains such an abundance of young canopy trees that the true undergrowth species are more than usually subordinate. One undergrowth species, however, *Sandwithia guyanensis* Lanjouw, forms as much as 24·4 per cent. of all trees under 4 in. (10 cm.) in diameter and over 15 ft. (4·6 m.) high. Only one of the canopy species forms an equally large proportion of the undergrowth. The floristic composition of the undergrowth (apart from the different relative abundance of the species) is much like that of the Morabukea and Greenheart consociations.

Both herb layers are represented by a large number of species and individuals, but social species or closed herbaceous vegetation of any kind are only found in openings. Tree seedlings are extremely abundant in the lower herb layer. Kakaralli (*Eschweilera* spp.) and Trysil (*Pentaclethra*) seedlings are the most abundant, but those of other species are also very common. *Cephaelis violacea* (Aubl.) and various Marantaceae are especially conspicuous in the tall herb layer, to which *Alsophila rostrata* (H.B.K.) and a few other tall ferns belong. The chief constituents of the small herb layer besides ferns (mainly *Adiantum* and *Lindsaya* species) are *Nautilocalyx lacteus* Sandwith (Gesneriaceae), a grass, *Ichnanthus panicoides* P. Beauv. and two small species of *Cephaelis* (Rubiaceae). Saprophytes are very rare.

Bush-ropes are more abundant than in any other type of forest.

All four societies of epiphytes are represented by many species and individuals. Though the general level at which they grow is high, yet members of the sun epiphyte society can commonly be seen from the ground.

The facies of the Mixed forest type which the sample plot represents is called by the Indians "Kakaralli bush." Another kind of Mixed forest, which we scarcely met with in our district, they call "Kautaballi bush": in this type of forest *Licania venosa* is more abundant and *Eschweilera* spp. less so than in "Kakaralli bush." "Kautaballi bush" is said to grow on lighter soils (verging on Greenheart sands) than "Kakaralli bush." A curious facies was met with on steep rocky hills with a shallow, sticky and heavy soil, like that of the facies of the Mora consociation found in similar places. This had a considerable proportion of *Mora excelsa*, though it was far from dominant. The abundance of ground ferns is characteristic. No doubt other facies of the Mixed forest could be recognised.

Mixed forest is the type always chosen by the Indians for cassava fields, and they prefer Kautaballi bush to Kakaralli bush. This is no doubt the reason why much of the ground where this type of forest would be expected bears only secondary forest. It is, however, difficult to distinguish old secondary forest from truly primary Mixed forest. Nevertheless, there can be little doubt that much of the Mixed forest, including our sample plot, was primary.

The Mixed forest association seems to have a wide distribution in the colony: in districts where loamy soils occur extensively it is usually the prevailing forest type.

(*d*) *Greenheart consociation.*

The Greenheart forests are one of the chief glories of British Guiana. There were characteristic specimens of this type in our district, though they were of very small area. The general aspect of a Greenheart forest is unmistakable. There are more trees of very large diameter than in any other type of forest: Mora is the only other type which approaches Greenheart in this respect. The greenish grey trunks of the Greenhearts rise very straight and columnar and are very little or not at all buttressed. Strongly buttressed trees among the subsidiary species stand out as exceptions. The scantiness of the undergrowth tree stratum is remarkable and makes it possible to see clearly for 30 or 40 m. ahead, a far greater distance than is possible in other types of forest. A characteristic feature is the large number of fallen logs, the abundance of the latter due to the Greenheart timber's extraordinary power of withstanding decay, rather than to a heavy mortality among the trees.

This consociation is, in our area, strictly confined to a single kind of soil, a sand nearly as light as that on which the Wallaba forest grows, but coloured reddish brown. The dead-leaf layer is about 2 cm. deep and is coloured dull brown. The top few centimetres of soil are whitish, not brown, and at the top of slopes, bordering on the Wallaba forests, the white layer may be thicker, but the heaps of soil by armadillo holes, etc., show that the subsoil is everywhere the same brown sand. The soil samples from the plot gave the following results:

Depth cm.	*p*H	Comber colour	KCl *p*H	Moisture at point of sticki-ness %	% of sand (1·0–0·04 mm.)	% of gravel (over 1 mm.)	Index of texture	Organic matter content %
0–20	4·35	Red	4·02	0	77·5	8·2	0 (light sand)	1·65
20–60	4·72	Light red	4·43	20·1	73·5	4·3	5 (sand)	—

Brown sands of this type are found chiefly on the slopes of the steep ridges, the flat tops of which are covered with white sand bearing Wallaba forest. The Greenheart consociation therefore occurs mainly in narrow strips (locally called "reefs").

Greenheart, *Ocotea Rodioei* (Schomb.) is clearly dominant. On the plot it forms only 9·4 per cent. of the trees above 4 in. (10 cm.) diameter, but 43·4 per cent. of trees over 16 in. (41 cm.). The percentage in the best Greenheart forests of the colony may be somewhat higher. The percentage in the different size classes are:

4–8 in. (10–20 cm.)	8–12 in. (20–31 cm.)	12–16 in. (31–41 cm.)	16–24 in. (41–61 cm.)	24 in. (61 cm.) and over
0·5 %	3·3 %	1·1 %	38·4 %	60 %

The small proportion in the size classes below 16 in. is a constant feature of the consociation: it is curious, considering that small saplings (under a metre) are fairly abundant, though they are not nearly as abundant, nor so evenly distributed as those of Mora, Morabukea or Wallaba in their respective consociations. Greenheart is found in all the other types of primary forest in small proportions (though in Wallaba it only occurs near the edge of its own consociation). Any forest containing over 150 cu.ft. per acre (equivalent to quite a small percentage) may be commercially workable and is therefore often spoken of as "Greenheart forest."

The subdominant trees are:

	Trees over 4 in. (10 cm.) diam.	Trees over 16 in. (41 cm.) diam.
Pentaclethra macroloba (Willd.) (Trysil)	9·1	3·8
Eschweilera Sagotiana Miers (Common Black Kakaralli)	7·6	7·0
Licania venosa Rusby (Kautaballi)	5·6	7·8

There are about ninety-one subsidiary species of canopy trees, the highest number in any plot. A certain number of these are probably characteristic of this type of forest. The proportion of Leguminosae is slightly less than in the Mixed forest (14 per cent.).

The undergrowth tree stratum, as already stated, is relatively scantily developed. Its floristic composition is much like that of the corresponding layer in the Mixed forest, but the great abundance (11·8 per cent.) of *Sandwithia guyanensis* Lanjouw is very characteristic. The Annonaceae, as usual, are abundant. Young canopy trees are far more abundant than true undergrowth species.

The fairly open canopy and scanty undergrowth make this a fairly light type of forest. Two measurements of illumination gave a mean value of 1/123

A =*Sandwithia guyanensis* Lanjouw
Ab =Broad-leaved Assipokoballi (? *Pouteria Jenmani* [Pittier]).
Af =Fine-leaved Assipokoballi (Sapotaceae).
Ai =Aiamorakushi (*Pouteria cladantha* Sandwith).
Ak =Akarako (*Marlierea Schomburgkiana* Berg.).
Ap =Adebero (*Paypayrola longifolia* Tul.).
Ar =Arara (*Unonopsis glaucopetala* R. E. Fries).
B =Baromalli (*Catostemma commune* Sandwith).
b =Baromalli (of Wallaba forest) (*C. fragrans* Bth.).
Bn =Baniaballi (? *Eugenia Arawakorum* Sandwith).
Br =Barataballi (Sapotaceae).
D =Duru (*Apeiba Petoumo* Aubl.).
Det =Determa (*Ocotea rubra* Mez).
F =Futui (*Jacaranda Copaia* [Aubl.]).
G =Greenheart (*Ocotea Rodiaei* [Schomb.]).
H =Haiariballi (Leguminosae).
Ix =*Ixora Schomburgkiana* Bth.
K 1 =Common Black Kakaralli (*Eschweilera Sagotiana* Miers).
K 2 =Fine-leaved Kakaralli (*E. Wachenheimii* [R. Benoist]).
K 3 =Smooth-leaved Kakaralli (*E. decolorans* Sandwith and/or *E. pallida* Miers).
K 4 =Wena Kakaralli (of Wallaba forest) (*E. corrugata* [Poit.]).
Ka =Kairiballi (*Licania heteromorpha* Bth. var. *perplexans* Sandwith).
Kb =Kautaballi (*L. venosa* Rusby).
Kh =Kurihikoyoko (*Anaxagorea dolichocarpa* Sprague et Sandwith).
Km =Large Kumaramara (*Duroia eriopila* L. *fil*).
Kr =Kurokai (*Protium decandrum* [Aubl.]).
Kt =Kauta (*Licania laxiflora* Fritsch).
M =Mabwa (? *Plumeria Sucuuba* Spruce *ex* Müll.-Arg.).
Mar =Marishiballi (of Wallaba forest) (*Licania buxifolia* Sandwith).
Mb =Manniballi (*Moronobea coccinea* Aubl.).
Ok =Broad-leaved Okokonshi (*Quiina indigofera* Sandwith).
Sb =Ginger Gale Silverballi }
Sb′ =Yellow Silverballi } Lauraceae.
Sh =Shibadan }
T =Trysil (*Pentaclethra macroloba* [Willd.]).
TT =Table Tree (*Cordia melanoneura* Klotzsch).
U =Unidentified.
W =Soft Wallaba (*Eperua falcata* Aubl.).
Wa =Waiaballi.
Wk =Warakusa (*Inga* sp.).
Wr =Warunanna (*Hortia regia* Sandwith).
Y =Fine-leaved Yarri-yarri (*Duguetia neglecta* Sandwith).
Yr =Yaruru (*Aspidosperma excelsum* Bth.).

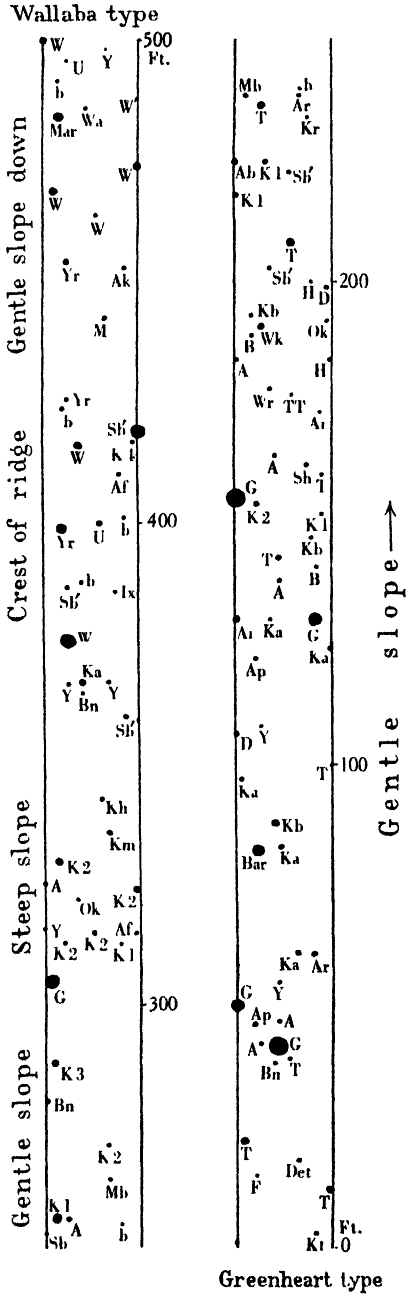

FIG. 1. Transect through the boundary between Wallaba and Greenheart forest on a hill-side. The belt was 500 ft. (152 m.) long and 20 ft. (6 m.) broad and ran approximately at right angles to the boundary between the two communities. Diameters of trees drawn approximately to scale.

of full light. This is considerably higher than either that of the Morabukea or the Mixed types, though much lower than in the Mora or Wallaba.

Corresponding with the high light values the herb layers are well developed, though closed vegetation is not found except in openings. Several species of Marantaceae are plentiful and conspicuous. The abundance of the ferns *Amphidesmium rostratum* (H.B.K.) and *Cyclodium meniscoides* (Willd.) is characteristic, though they also occur in other types of forest. The occurrence of *Centrosolenia densa* (C. H. Wright) is noteworthy: it is one of the most constant and conspicuous species of the Wallaba consociation. The general floristic composition of the herbaceous vegetation is, however, on the whole, much like that of the Morabukea and Mixed types. Saprophytes are scarce.

Epiphytes, as would be expected from the lightness, grow at fairly low levels. Tillandsias were twice observed at less than 2 m. from the ground. Other sun epiphytes were also noted at similar levels.

Greenheart is a species almost endemic in British Guiana. It has been recorded in Surinam and in Venezuela, but in both cases not far from the frontier. In the North-West District it is extremely local and is known in small quantity in two localities only. Probably true Greenheart forest is found only towards the centre of the range of the species. The finest and most extensive Greenheart forests seem to be in the lower Mazaruni valley (e.g. in the neighbourhood of Ikuribisi Creek). It is not known what type of forest replaces it outside the range of the species.

(*e*) *Wallaba consociation.*

The most distinctive of all the types of forest is the Wallaba consociation dominated by *Eperua falcata* Aubl., which is found on the white sand of the high hill ridges. Both structurally and floristically it is much more sharply distinguished from the other types of forest than they are from one another. In some of its characteristics it seems to approach monsoon forest (e.g. it has a larger proportion of deciduous trees than the other types). Three features help to produce the characteristic appearance of this consociation, the extraordinarily large number of trees per unit area (919 trees over 4 in. (10 cm.) on the plot, or nearly twice the number on the Mora plot), the scarcity of very large trees (only four over 24 in. (61 cm.) diameter on the plot, as compared with twenty-nine on the Greenheart or nine on the Mixed plot) and the almost complete absence of buttressed trees. The dominant is itself completely unbuttressed and none of the subsidiary species is more than slightly buttressed. The bright light and comparatively dry atmosphere (cf. Table VI, Part I) make the Wallaba forest much the pleasantest type to work in. The former feature is reflected in the low level to which the epiphytes commonly descend, a fact which has already been discussed (Part I, p. 382), indeed they seem to be more abundant below the canopy than in it. To the low humidity is related the remarkable scarcity of epiphyllous liverworts and of shade epiphytes in general.

The porous white sand on which the Wallaba forest grows covers the level tops of all the ridges higher than about 50 m. to a considerable depth. In our district these ridges were mostly narrow (a few hundred metres across), but in some parts of the colony they broaden out into wide plateaux. The edge of the white sand areas is always very sharp and the boundary of the Wallaba consociation coincides exactly with that of its own particular soil. Wood gives a pretty instance of this from the Bartica-Kaburi district: "...In most cases it was possible to step in one stride from the white sand where the Greenheart never occurred[1] to the brown soil where it did, generally at some point on the slopes down from the flat ridge to the creeks. The most striking instance was seen...where a nest of Akushi [leaf-cutting] ants had thrown up the soil over an area about 30 ft. square. On the upper half of the nest the soil was white, on the lower half brown and the dividing line was sharp enough to lay a hand across. Two trees were growing out of the nest so close together that a man would have to go sideways to pass between and they occurred one just on the white soil and the other just on the brown soil below. The upper tree was the last Wallaba and the lower the first Greenheart on that slope" (**1**, pp. 4–5). A belt transect showing the abrupt transition from the Wallaba to the Greenheart type is given in Fig. 1.

The carpet of dead leaves has a characteristic mottled colour: the dead Wallaba leaves are nearly black, those of the other trees are a very light dull brown. It is extremely thin, averaging 1·5 cm. thick. The soil on the other hand is stained dark brown by humus to an unusual depth, humus particles being visible to 16 cm. and a distinct brown stain to 25 cm. Below this the pure white sand was traced to 1·83 m. and no doubt could have been followed much deeper. The results of analysis were:

Depth of sample cm.	*p*H	Comber colour	KCl *p*H	Moisture at point of stickiness %	Organic matter content %	% of sand (1·0–0·04 mm.)	% of gravel (over 1 mm.)	Index of texture
0–25	4·75	Colourless	3·72	Nil	1·36	69·2	5·3	Nil (light sand)
25–85	4·88	Colourless	4·60	Nil	—	90·0	2·9	Nil (light sand)

This sand was formerly thought to be wind-borne, but is more probably produced by the degradation of granite and gneiss *in situ*[2]. The absence of colour with Comber's thiocyanate test in spite of high acidity shows that this soil is extremely deficient in iron.

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[1] Greenheart occurred in small quantity in the Wallaba forests of our district, probably because the white sand covering of the ridges was rather thin.

[2] The late Sir John Harrison wrote in a report dated 20th December, 1915, after studying the similar white sands of Surinam: "Evidence was obtained which clearly pointed to their being residual deposits arising from the weathering of granitic rocks *in situ* and not, as frequently asserted, dune-sands or clastic water-borne sands."

The Soft Wallaba (*Eperua falcata* Aubl.) is overwhelmingly dominant, forming 21·1 per cent. of all trees over 4 in. (10 cm.) diameter and 67 per cent. of those over 16 in. (41 cm.). The percentages in the separate size classes are:

4-8 in. (10-20 cm.)	8-12 in. (20-31 cm.)	12-16 in. (31-41 cm.)	16-24 in. (41-61 cm.)	24 in. (61 cm.) and over
10 %	17·3 %	32·7 %	66·7 %	75 %

Eperua falcata grows in all the types of forest. Outside its own type it has a secondary maximum of abundance in the Mora forest. This distribution seems to suggest that it is a light demander. Benoist (**6**) mentions it as one of the principal species in the swamp forests in French Guiana. It is a somewhat curious fact that closely allied species of *Eperua*, the Ituri Wallabas, *E. Jenmani* Oliv. and *E. grandiflora* (Aubl.), are among the most abundant (though not subdominant) of the subsidiary species in the Wallaba consociation. They reappear as rare species in the Mora forest, and still more rarely in the "central" types.

The regeneration of the dominant in the Wallaba forest is ample, but dense thickets of seedlings are not formed as in Mora and Morabukea forest. Counts on six square metres taken at random gave an average of 1·8 seedlings under 2 m. high per square metre. They were much less abundant in the openings and better lit places.

The subdominants are *Catostemma fragrans* Bth. (Wallaba Baromalli) 15·1 per cent. of trees over 4 in. and 3 per cent. of those over 16 in. diameter, and *Licania buxifolia* Sandwith (Wallaba Marishiballi) 12·2 and 4 per cent. The seedlings of the former are nearly as abundant as those of the dominant (1·1 per sq. m.), but those of the latter are considerably scarcer than those of *Cassia pteridophylla* Sandwith (Immirimiaballi), the most abundant of the subsidiary species. Both these subdominants are strictly characteristic of the Wallaba consociation in our area and are never found elsewhere. There were approximately seventy-one subsidiary tree species over 4 in. (10 cm.) diameter. A large proportion of these, perhaps 25 per cent., are confined to this type of forest. There are no tall palms though young plants without trunks of *Jessenia oligocarpa* Griseb. et H. Wendl. are abundant everywhere.

Approximately 53 per cent. of the trees over 4 in. (10 cm.) diameter are Leguminosae (including the dominant).

The stratum of undergrowth trees is dense, but much less well defined than in the other types of forest. It consists chiefly of a thicket of young canopy trees of very irregular heights (indeed it is scarcely marked off at all from the tall herb stratum). True undergrowth trees are few in individuals and very few in species. The floristic composition of the layer is peculiar, as some species, e.g. Kurihikoyoko, *Anaxagorea dolichocarpa* Sprague et Sandwith, which occur in every other type of forest, are absent and there are several species strictly characteristic of the consociation, one of which, *Ixora Schomburgkiana* Bth.[1], was frequent. The most abundant species, *Marlierea*

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[1] One tree of this species was seen in the "Dakamaballi facies" of Mora forest described on p. 113.

Schomburgkiana Berg. (Akarako) and *Ecclinusa psilophylla* Sandwith each formed 7·4 per cent. of the trees under 4 in. diameter and over 15 ft. (4·6 m.) high.

In spite of the dense growth of young trees, Wallaba is the lightest type of forest, the average illumination at breast-height (six measurements) being 1/70 of that in the open. The illumination is fairly even and there is little deep shade.

In view of these facts it is hard to understand why the herb strata should be represented by fewer species than that of any other types of forest and by fewer individuals than that of any type but Morabukea. Colonies of closed ground vegetation are sometimes found, however, but only in the rather frequent slight openings. The floristic composition of the herbaceous vegetation is interesting. It contains four distinct elements: (i) species peculiar to the Wallaba type, *Triphora amazonica* Schlecht., *Cephaelis dichotoma* Rudge; (ii) species found outside the Wallaba type only in secondary forests or clearings, *Bromelia Karatas* L., a plant which forms impenetrable thickets several square metres in area, *Centrosolenia densa* (C. H. Wright) (this also occurred in Greenheart forest), *Heliconia Ballia* L. C. Rich.; (iii) species found outside the Wallaba type only in Mora forest, *Monotagma Parkeri* (Roscoe) (not on plot), *Trichomanes arbuscula* Desv., *Piper moraballianum* Trel., *Leiphaimos aphylla* (Jacq.) (though one specimen of this was once found in Morabukea forest), (iv) species found in all the other types of forest, e.g. *Leiphaimos corymbosa* (Splitg.), *Schizaea fluminensis* Miers, *Ischnosiphon surinamensis* (Miq.), *Selaginella Parkeri* (Hook. et Gr.), *Amphidesmium rostratum* (H.B.K.). Many of the common species in the four other types of forest are quite absent in the Wallaba type. Besides the above species there are a few which do not come exactly under any of the above heads.

Group (ii) are presumably merely light demanders. (iii) may be also light demanders, but they are probably also sand lovers as they only grow in the parts of the Mora forest with a sandy surface soil (mainly in the "Dakamaballi facies").

Bush-ropes are scarcer than in any other type of forest. As Chipp noticed in the driest type of closed forest in the Gold Coast (7, p. 51), they usually ascend straight to the canopy without any loose coils. Some of the species are probably characteristic of the consociation, e.g. *Arrabidaea candicans* (Rich.) and *Mascagnia leucanthele* (Gr.) *em* Niedenzu.

The Wallaba forest of the Moraballi district is all extremely uniform. *Eperua falcata* has a wide distribution. It is found throughout the greater part of British Guiana and extends eastwards to the State of Para in Brazil. The Wallaba type of forest has a wide distribution in the colony near the coast and probably also occurs in the interior. It is absent in the North-West District except in the small area where white sand soils are found. No doubt it also occurs in Surinam, etc., but we have no definite information on the subject. The "caatinga" forests on white sand plateaux in the Rio Negro region (not to be confused with the "caatinga" forests of South Brazil, which are deciduous forests occurring in Savannah regions) seem to correspond closely with our Wallaba consociation, according to Spruce's description (**8**, vol. **1**, pp. 206–7 and 303–4). The flora of the two is closely related, but nothing is known as to the proportions in which the species occur in the "caatingas."

On extensive white sand plateaux the Wallaba forest is often replaced over large areas by Dakama forest (dominant *Dimorphandra conjugata* [Splitg.]?) or by a kind of scrub called "Muri," dominated by *Houmiri floribunda* Mart. Both these types of vegetation are found in the Bartica-Kaburi region not many miles from Moraballi Creek and it is not unlikely that we should have met with them if we had penetrated to the head-waters of our creek on the Essequibo-Demerara watershed.

In some parts of the interior of the colony (e.g. the Kaburi district) the forests of *Eperua falcata* are replaced by those of Clump Wallaba (*Dicymbe corymbosa* Bth.), which often has a considerable admixture of *Eperua falcata.* This extraordinary tree has the habit of self-pollarding, so that most of the mature trees are replaced by a large clump of slender pollard stems. This community sometimes occurs also on clay soils.

(3) *Buttressing of trees.*

One of the most striking differences between the five forest types is in the proportion of buttressed trees and the size of the buttresses. The enormous plank buttresses are the chief feature of the Mora forest: passing through the series of types buttressing decreases till in the Wallaba forest it has practically disappeared. This generalisation applies both to the dominants and to the subordinate species. Mora is always a strongly buttressed tree, Wallaba is unbuttressed or shows only the slightest trace of buttresses (cf. Pl. XII, phot. 1; Pl. XIII, phots. 3 and 4). Morabukea, Kakaralli and Greenheart show intermediate conditions. The proportion of unbuttressed subordinate species increases regularly from Mora with few to Wallaba with nearly all. For want of a means of expressing these facts quantitatively (which would be difficult as both the proportion of buttressed individuals and the size of the buttresses is involved) an attempt has been made to illustrate them by scaled drawings (Fig. 2). The inevitable deduction is that buttressing is related to edaphic factors.

Till lately buttresses have usually been considered as modifications to allow the trees to stand strains due to wind. Whitford (**5**) has given what is probably the fullest account of this view. Navez (**9**) writing of the Rio de Janeiro district also accepts it, suggesting that the trees have the more need for support as the soil of the rain forest offers little resistance, being deep and formed of innumerable dead leaves: this is surely an unusual condition in tropical forests and it was certainly never observed by us in the Moraballi area.

Phot R. W. G. Hingston

Phot. 6. A stilt-rooted tree (*Tovomita* sp.).

Phot. R. W. G. Hingston

Phot. 5. A greenheart logging trail through Sandy Mora forest. The palm is a young (stemless) plant of *Jessenia oligocarpa* Griseb. et H. Wendl.

DAVIS AND RICHARDS—MORABALLI CREEK

Face p. 126

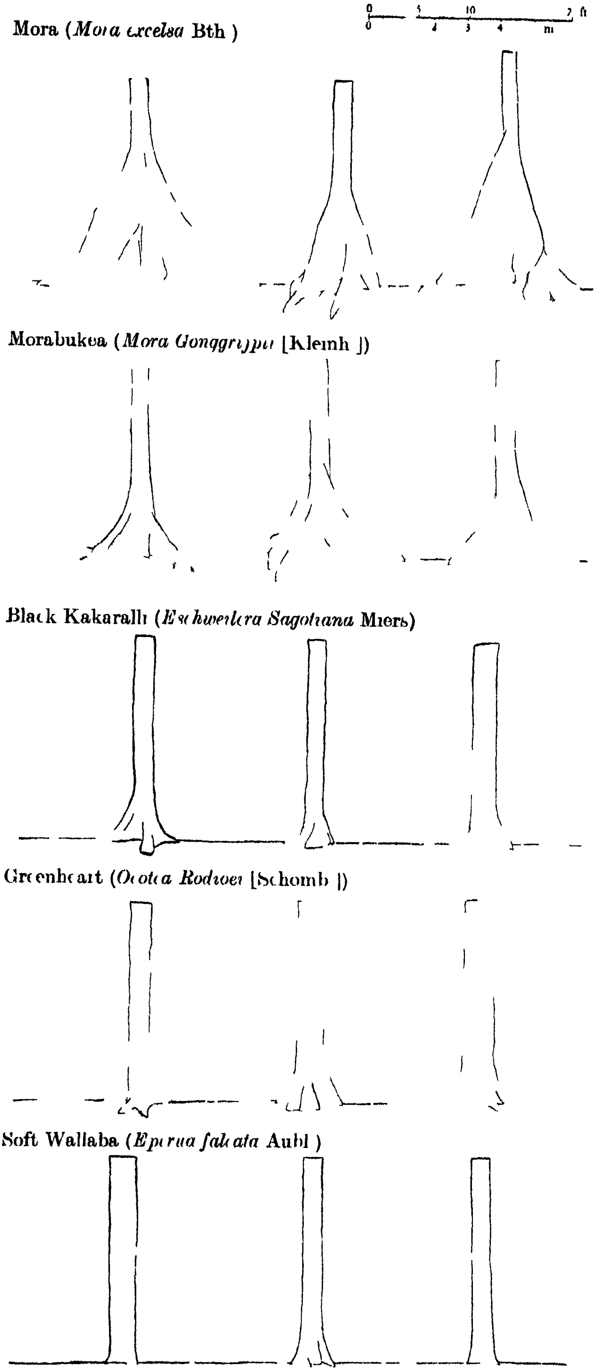
Mora (*Mora excelsa* Bth.)
0 5 10 20 ft
0 2 3 4 m
Morabukea (*Mora Gonggrijpii* [Kleinh.])
Black Kakaralli (*Eschweilera Sagotiana* Miers)
Greenheart (*Ocotea Rodiaei* [Schomb.])
Soft Wallaba (*Eperua falcata* Aubl.)

Fig. 2. Buttresses of typical mature individuals of the dominant trees in each forest type. Drawn to scale in the field.

Lately some very serious objections to this long-established view have been brought forward independently by Petch (**10**) and Francis (**11**) who worked in Ceylon and Queensland respectively. The chief of these are:

(i) There is no evidence that the development of buttresses is correlated with the weight of the crown of the tree. Our observations at Moraballi Creek fully confirm this statement. Three of the most common species of tree which normally have their whole crowns raised clear above the canopy (and their crowns are exceptionally broad and heavy) are *Peltogyne pubescens* Bth. (Purpleheart), *Hymenaea Courbaril* L. (Locust) and *Couratari pulchra* Sandwith (Wadara). The first has well-developed and spreading, but not exceptionally large, buttresses; the second none at all; the third has fairly large buttresses, but they are high and do not spread far out from the trunk, so cannot be very effective mechanical supports.

(ii) There is no relation between the direction of the prevailing winds and the orientation of the buttresses. This is also true in Guiana where the direction of the wind is extraordinarily constant[1].

(iii) Buttresses often appear in young trees when they are still under the shelter of the canopy. This is certainly true for the majority of the buttressed trees in our district, but it seems a less good argument than (i) or (ii), for the appearance of an organ earlier in ontogeny than it can be useful is no argument against its value to the mature organism. We found, however, that the true undergrowth trees, which never reach the canopy, were never buttressed.

To these objections we would add the following:

(i) The height of the trees in tropical forests has been exaggerated in the past. The average height of canopy trees in our Mixed type of forest is about 30 m. and even in the Mora type it is probably not more than 40 m. These heights are not so much greater than those found in extra-tropical forests as to demand a special adaptation for mechanical support, particularly as the trees of the canopy are often so closely bound together by bush-ropes as to support one another even when cut through at the base. In Guiana, at least, violent winds are not as common as in temperate regions. Moreover, in the types of forests in which buttresses are most developed the soil is exceptionally hard and resistant, while in the Wallaba type where they are almost absent the soil is soft and loose.

(ii) The type of forest with the most developed buttressing is found on the bottoms of sheltered creek valleys, while the type with the least development is confined to the exposed ridges and plateaux. It is interesting to note that Whitford (though defending the mechanical support view) observed a similar state of affairs in the Philippines. Speaking of *Parkia* he says "...higher up the mountain the buttress habit is present, but not so prevalent; it disappears altogether on the exposed ridges of the mountain" (**5**, p. 420).

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[1] Navez (**12**), however, found in Cuba that there was a statistically significant correlation between the direction of the prevailing wind and the most frequent orientation of the buttresses in *Ceiba pentandra* Gaertn.

We are not trying to deny that buttresses, when present, are not efficient mechanical supports, but merely to suggest that the need for mechanical support has not been the primary cause for their development.

Petch (**10**) suggests that the formation of buttresses depends on the absence of a tap-root which is due to shallowness of soil produced by water-logging on low-lying ground and stoniness on slopes.

Our observations on the distribution of buttressing in the Guiana forest would seem to fit in very well with this theory. They show that as the soil becomes lighter in texture (and therefore more penetrable), the amount of buttressing of the trees decreases. We unfortunately have no data on the occurrence of tap-roots, but all our observations of uprooted trees tend to show that they are very shallow rooted and that in most cases the bulk of the roots lie in the top metre or less of soil. Further, many trees which are not buttressed have surface roots. The most remarkable example is the Souari-nut tree, *Caryocar nuciferum* L., whose large lateral roots run just above the surface of the ground often for 10 or 15 m. Another piece of evidence for the theory is the fact that the most buttressed type of forest, Mora, is found either on the swampy flood-plain *or* on stony hill sides. The shallowness of the soil ("physiological" in the first habitat, actual in the second) is the only common factor of the two habitats which can explain such a distribution.

It must not be forgotten that buttressing is to a large extent a hereditarily fixed character, as Francis (**11**) has pointed out. A young buttressed tree which happens to be growing on a deep soil presumably will not cease to produce buttresses, nor will a normally unbuttressed species develop them if it happens to be growing in a swamp though there may be a certain amount of plasticity in this respect. Hence buttressed species occur in habitats where most of the trees are unbuttressed and *vice versa.*

The immediate cause of buttress formation, according to Petch, is the restriction of food and water conduction mainly to limited narrow tracts continuous with the lateral roots, assuming that there is very little transverse conduction in the trunk. It may be pointed out that this assumption receives some justification from the recent remarkable experiments of Caldwell (**13**).

Stilt-rooting (i.e. formation of "flying" buttresses) seems to be related to different conditions from plank-buttressing as the few stilt-rooted species in our district, e.g. *Tovomita* spp. and *Clusia* spp. with round stilts, *Virola surinamensis* (Rol. *ex* Rottb.) (Dalli) and *Protium decandrum* (Aubl.) (Kurokai) with flat stilts are found in about equal numbers in all the five types of forest.

(4) *Comparison of types and discussion.*

When the main data about the types of primary forest which have just been described are compared, as in Table I, some very striking regularities appear. The five types are there arranged in the order in which they have been described, which is the most usual order in which they are met with on passing from the flood plain to the hill ridges. This natural sequence is not invariable because it depends only on the sequence of soils and may be upset by local variations in the topography.

Table I. *Comparison of sample plots.*

	Mora	Mora-bukea	Mixed		Greenheart	Wallaba
Soil (lower sample) ...	Fine silt	Heavy silt	Light loam		Sand	Light sand
Index of texture	40	44	18		5	0
Moisture at point of stickiness	47·5	49·1	28·1		20·1	Nil
Illumination	1/75	1/163	1/150		1/123	1/70
Saturation deficit of air in undergrowth (not measured actually on plots)	High		Intermediate			Low
Dominant or most abundant species	*Mora excelsa* Bth.	*Mora Gonggrijpii* (Kleinh.)	*Eschweilera Sagotiana* Miers	*Licania venosa* Rusby	*Ocotea Rodioei* (Schomb.)	*Eperua falcata* Aubl.
As percentage of trees over 4 in. (10 cm.) diameter	23·4	26·6	6·1	9·5	9·4	21·1
As percentage of trees over 16 in. (41 cm.) diameter	67·2	60·7	15·6	11·1	43·4	67·0
Number of trees per hectare:						
Over 4 in. (10 cm.) diameter	310	309	432		519	617
Over 16 in. (41 cm.) diameter	45	60	60		87	67
Number of tree species over 4 in. (10 cm.) diameter	60	71	91		95	74
Percentage of Leguminosae (individuals)	59	33	15		14	53
Buttressing of dominant	Very strong	Strong	Slight		Very slight	None
Abundance of strongly buttressed subsidiary species	Abundant	Frequent	Occasional		Scarce	Rare

As the series is followed from the Mora forest of the flood-plains to the Wallaba forest of the white sand plateaux, there is at first the strong dominance of a single species, then a decline, till in the Mixed forest it is impossible to speak of the clear dominance of one species: after this point dominance increases again till at the end of the series dominance is exactly as strong as at the beginning. Now the climatic factors acting on these forest types are practically the same throughout the series (neglecting very slight differences in exposure to wind). The acidity of the soil is approximately the same in all: nothing is known of other "chemical" edaphic factors, but they are not likely to differ much as all the soils are derived from the same parent rock. The physical characters of the soil, on the other hand, do vary regularly.

The depth of the soil increases regularly up the series: the index of texture diminishes. It seems very probable that it is some factor or complex of factors dependent on these physical characteristics of the soils which determines the series of forest types. The fact that the proportion of Leguminosae, i.e. of plants not dependent on the nitrogen in the soil, varies in a regular manner, suggests that the physical factors may act by affecting nitrification.

If the five types are compared floristically it is seen that the list of species is very similar in all. Many species are found in all, or at least five, of the plots; the differences lie largely in the proportions in which they occur. The types at each end of the series, Mora and Wallaba, are, however, rather sharply marked off from the rest and the three types in the middle are rather closely alike—this is especially well seen in the herb layers. The types at each end also resemble one another in certain respects, mainly because of the high light intensity in the undergrowth. They have therefore been grouped together as the "extreme" types and the three middle members as the "central" types.

As the number of trees per unit area increases regularly from Mora to Wallaba it might be concluded that the Wallaba forest occupies the optimum habitat in the series and that conditions become progressively less favourable towards the Mora habitat. Since, however, the average diameter[1] of the trees decreases as the number per unit area increases, it seems unlikely that the number of trees per unit area is a good index of the favourability of the habitat.

The white sands on which the Wallaba forest occurs are white owing to the absence of iron (see above, p. 123). Since iron is present in the other soils derived from the same rock it has presumably been removed from the white sand by intense leaching. If the Wallaba soils are deficient in iron they are probably still more deficient in the more soluble plant nutrients and are therefore probably a less favourable soil than the brown loam of the Mixed forest, which contains abundant iron and is presumably less leached. The brown sands of the Greenheart forest are probably intermediate in this respect. There can be little doubt that the Mora forest also occupies a less favourable soil than that of the Mixed forest, owing to its extreme shallowness (cwing either to water-logging or to stoniness). Here again the Morabukea soil is intermediate.

We are therefore probably justified in concluding that the Mixed forest occupies the optimum habitat and that the forest types with a high degree of dominance occupy less favourable habitats, a result which might perhaps have been expected.

This series of forest types is of interest from the point of view of vegetation classification. Though it would be premature to fit it into a definite scheme, the following view may be suggested provisionally.

All five types are undoubtedly primary in the sense that they do not belong to any secondary succession. As the Mixed forest association occupies the optimum habitat it must be regarded as the climatic climax of the district. The Mora and Wallaba consociations are, however, equally climax types. They cannot be considered less highly developed and there is no reason for believing that the soils on which they are found are not mature or that they show any tendency to become similar to the Mixed forest soil: they are therefore probably best regarded as edaphic climaxes. The Morabukea and Greenheart consociations can then be considered either as independent types connecting the climatic climax with the two edaphic climaxes or perhaps merely as well-marked facies of the climatic climax approaching the edaphic climaxes in certain characteristics.

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[1] This decrease in size is obvious in the field and can also be made out in a general way in Tables I–V, but cannot be easily expressed quantitatively from the data available. It is probably accompanied by decrease in average height, but we have not enough measurements to show that.

The status of "Low Bush" has already been discussed. The regularities shown in Table VI are striking enough to give strong confirmation to our conclusion that all five forest types are in their primitive condition. "Low Bush," which occurs on a wide range of soils, could have no place in the series, a fact which tends to support the view that it belongs to a secondary succession.

It is hardly necessary to point out that the deductions in this last section are very tentative and are only put forward as working hypotheses for future research.

II. SUMMARY.

1. The primary forest of the district is not homogeneous, but consists of five distinct communities, the Mora (dominant, *Mora excelsa* Bth.), Morabukea (dominant, *Mora Gonggrijpii* [Kleinhoonte]), Mixed (no clear dominant), Greenheart (dominant, *Ocotea Rodioei* [Schomb.]) and Wallaba (dominant, *Eperua falcata* Aubl.) types. The floristic composition of each was analysed by counts of trees on sample plots.

2. Each type of forest is more or less clearly limited to a definite type of soil. If the types are arranged in order from the type on the wettest (Mora) to the one on the driest soil (Wallaba) some striking regularities are disclosed. Dominance of a single species of tree is marked at each end of the series (67 per cent. of all over 41 cm. diameter) and decreases regularly to a minimum at the middle. The number of trees on unit area increases steadily from Mora to Wallaba. The number of species of trees on the sample plots is greatest in the Mixed and Greenheart forest and considerably smaller in the other types. The proportion of Leguminosae is high at each end of the series and diminishes towards the middle.

3. The buttressing of the trees is greatest in the Mora type and diminishes with great regularity to the Wallaba. This fact supports the views of Petch and is quite contrary to any teleological interpretation of their significance. Other facts are given which point in the same direction.

4. All five types of forest are climax communities, but the Mixed type probably occupies the optimum habitat and should be regarded as the climatic climax of the district.

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NOTE. TABLES II–VI.

The vernacular names of trees given are those used by the Arawak Indians of the Pomeroon River. Where trees have well-known Creole names these are given instead and are indicated by being placed in brackets [ ].

Specific names are given for plants which were actually collected *in the Expedition's area* (not necessarily in the plots). Where there is doubt as to the identity of the plant collected and the plant found on the plot a query is placed *in front of the generic* name. Where the identification of the specimens collected is in doubt a query is put *after the specific* name. In a few cases though no material was collected the identity of the species is fairly certain: the scientific name is then given in brackets [ ].

It must be remembered that the identifications of vernacular names given in the following tables apply only to our area and the same vernacular name may be applied to a different species in other parts of the Colony.

In Tables II and IV–VI the plants on each plot are enumerated under three categories, viz. "I. Trees over 4 in. [10 cm.] diameter." "II. Trees under 4 in. [10 cm.] diameter and over 15 ft. [4·6 m.] high." "III. Plants under 15 ft. [4·6 m.] high." I includes all the canopy trees and exceptionally large trees of the undergrowth stratum; II includes the bulk of the undergrowth tree stratum; III the two mainly herbaceous layers. With III (i) the shrub and tall herb layer are included many species which belong when mature to the undergrowth stratum, for they often flower long before reaching their full size.

The diameters of trees given were measured at breast height *or* above the buttresses.

Table II. *Sample Plot I. Mora consociation.*

I. Trees over 4 in. (10 cm.) diameter (on whole plot, 400 × 400 ft. [122 × 122 m.]).

Vernacular name	Species	Diameter class					Total number of individuals over 4 in. (10 cm.) diam.
		4–8 in. (10–20 cm.)	8–12 in. (20–31 cm.)	12–16 in. (31–41 cm.)	16–24 in. (41–61 cm.)	24 in. (61 cm.) and over	
Akarako	Marlierea Schomburgkiana Berg	1	–	–	–	–	1
Arara	Unonopsis glaucopetala R. E. Fries	5	–	–	–	–	5
Arisauro	[Leguminosae]	–	1	–	1	–	2
Arumatta	Clathrotropis brachypetala (Tul.)	9	3	2	1	–	15
Assipokoballi, "Fine Leaf"	[Sapotaceae]	1	–	–	–	–	1
Awassakuli, "Large Leaf"	Tovomita obovata Engler	2	–	–	–	–	2
Awassakuli, "Small Leaf"	Tovomita or Clusia sp.	1	–	–	–	–	1
Baradan	[Lauraceae]	–	–	1	–	–	1
Barataballi	[Sapotaceae]	–	1	–	–	–	1
Baromalli	Catostemma commune Sandwith	8	5	1	2	1	17
[Corkwood]	[Pterocarpus officinalis Jacq.]	10	24	9	4	–	47
[Crabwood]	[Carapa guianensis Aubl.]	1	1	–	–	–	2
Dalli	Virola surinamensis (Rol. *ex* Rottb.)	1	2	–	1	–	4
Dakamaballi	Aldina insignis (Bth.)	7	10	5	4	1	27
Duka (= Waramia)	Tapirira Marchandii Engler	–	3	–	–	–	3
Dukali	—	1	–	–	–	–	1
Fukadi, "Broad Leaved"	Terminalia Tanibouca Rich.	5	2	2	–	–	9
[Greenheart]	Ocotea Rodioei (Schomb.)	3	1	1	2	–	7
Kakaralli, "Common Black"	Eschweilera Sagotiana Miers	9	1	–	–	–	10
Kakaralli, "Smooth Leaved"	E. decolorans Sandwith E. pallida Miers	11	3	–	–	–	14
Kakaralli, Wena (of swamps)	E. longipes (Poit.)	11	6	1	–	–	18
Karahoro	Didymopanax Morototoni (Aubl.)	2	–	–	–	–	2
Kauta	Licania laxiflora Fritsch	1	–	–	–	–	1

Kirikowa	Iryanthera paraensis Hub.	–	1	–	–	–	1
Kurokai	[Protium decandrum (Aubl.)]	7	4	–	–	–	11
Maho, "Fine Leaved"	Sterculia pruriens (Aubl.)	4	1	–	–	–	5
Manni	[Symphonia globulifera L. fil]	1	–	–	–	–	1
Manniballi	Moronobea coccinea Aubl.	1	–	1	–	–	2
[Monkey Pot] or Wadaduri	Lecythis Davisii Sandwith	3	1	–	–	–	4
Mora	Mora excelsa Bth.	28	19	17	24	21	109
Moraballi	Pouteria minutiflora (Britton)	–	1	–	–	–	1
Okokonshi, "Broad Leaf"	Quiina indigofera Sandwith	1	–	–	–	–	1
Sarabebe	Macrolobium bifolium (Aubl.)	4	2	–	–	–	6
Saramakushi	—	–	1	–	–	–	1
Serebedan	[Swartzia sp.?]	1	–	–	–	–	1
Shirabuliballi	Sloanea amplifrons Johnston	1	–	–	–	–	1
Shirua	—	1	–	–	–	–	1
Silverballi, "Ginger Gale"	[Lauraceae]	1	1	–	–	–	2
Suradan	Hieronyma laxiflora Mull.-Arg.	1	–	–	–	–	1
[Trysil]	Pentaclethra macroloba (Willd.)	22	20	3	2	–	47
Wallaba, "Soft"	Eperua falcata Aubl.	2	4	2	1	–	9
Waiaballi	—	–	1	–	–	–	1
Warahaia	[Melastomaceae]	5	6	–	–	–	11
Warakusa	Inga spp.	6	3	2	–	–	11
[Water Sawarri] or Kola	[Caryocar glabrum (Aubl.)]	–	1	–	–	–	1
[Wild Maran] or Kunoribi	[Guttiferae]	1	–	–	–	–	1
Yaruru	Aspidosperma excelsum Bth.	–	–	1	2	–	3
[Unknown, "A"]	Sandwithia guyanensis Lanjouw	2	–	–	–	–	2
[Unknown, "D"]	Mabea Piriri Aubl.	1	–	–	–	–	1
[Unknown, "Y"]	—	1	3	–	–	–	4
[Unknown (like Duka)]	—	1	–	–	–	–	1
[Unknown (like Suradan)]	[Euphorbiaceae]	8	–	–	–	–	8
[Unknown]	[Melastomaceae]	5	6	–	–	–	11
[Unknown]	—	–	1	–	–	–	1
[Unknown]	[About 5 species]	9	2	–	–	–	11
	Totals	206	141	48	44	23	462
			Total number of trees over 16 in. (41 cm.) diameter				67

Table II (*contd.*).

II. Trees under 4 in. (10 cm.) diameter and over 15 ft. (4·6 m.) high (on two strips each 25 × 400 ft. [7·6 × 122 m.]).

Vernacular name	Species	No. of individuals
Arara	Unonopsis glaucopetala R. E. Fries	1
Arumatta	Clathrotropis brachypetala (Tul.)	1
Awassakuli, "Large Leaf"	Tovomita obovata Engler	1
Awassakuli, "Small Leaf"	Tovomita or Clusia sp.	2
[Corkwood]	[Pterocarpus officinalis Jacq.]	1
Dakamaballi	Aldina insignis (Bth.)	7
Fukadi, "Broad Leaved"	Terminalia Tanibouca Rich.	1
[Greenheart]	Ocotea Rodioei (Schomb.)	1
Kakaralli, "Common Black"	Eschweilera Sagotiana Miers	5
Kakaralli, "Smooth Leaved"	E. decolorans Sandwith E. pallida Miers	9
Kakaralli, Wena (of swamps)	E. longipes (Poit.)	1
Kautaballi	Licania venosa Rusby	1
Kurihikoyoko	Anaxagorea dolichocarpa Sprague et Sandwith	11
Kurokai	[Protium decandrum (Aubl.)]	1
Mora	Mora excelsa Bth.	15
Silverballi, "Brown"	Nectandra sp.?	1
[Trysil]	Pentaclethra macroloba (Willd.)	13
Wallaba, "Soft"	Eperua falcata Aubl.	1
Warakusa	Inga spp.	3
Yarri-yarri	Duguetia neglecta Sandwith D. pycnastera Sandwith	9
[Unknown, "A"]	Sandwithia guyanensis Lanjouw	3
[Unknown (like Duka)]	—	1
[Unknown (like Suradan)]	[Euphorbiaceae]	1
[Unknown]	[Melastomaceae]	1
[Unknown]	[4 species]	7
	Total	98
Palms: Manicole	[Euterpe edulis Mart.]?	14
Turu	Jessenia oligocarpa Griseb. et H. Wendl	1
	Total	15

III. Plants under 15 ft. (4·6 m.) high (omitting young trees and bush-ropes).

(i) Layer of shrubs and tall herbs	Swampy ground	Drier ground
Aciotis laxa (Rich.)	f.	–
Alsophila rostrata (H.B.K.)	–	o.
Bactris simplicifrons Mart.	v.r.	o.
Bactris sp.	–	r.
Carludovica sp.	a.—f.	–
Cephaelis tomentosa (Aubl.)	o.	–
C. violacea (Aubl.)	v.r.	o.
Clidemia conglomerata (Rich.)	–	r.
Cordia nodosa Lam.	–	r.
Duguetia neglecta Sandwith D. pycnastera Sandwith	v.r.	o.
D. Yeshidan Sandwith	v.r.	f.
Geonoma robusta Burret	–	o. (young)
Hemitelia strigosa (J.Sm.)	v.r.	v.r.
Ischnosiphon Arouma (Aubl.)	o.	o.
I. surinamensis (Miq.)	–	o.
Miconia Plukenetii Naud.	v.r.	–
Montrichardia aculeata Crug.	l.f. (opening)	–
Piper moraballianum Trel.	–	v.r.
P. Miquelii C.DC.	v.r.	r.
P. flexuosum Rudge	–	v.r.
Sabicea glabrescens Bth.	r. (opening)	–
Spathiphyllum cuspidatum Schott.	o.	v.r.
Tabernaemontana undulata Vahl	–	o.
Tococa aristata Bth.	r.	o.
Urospatha sagittifolia (Rodsch.)	o.	–
—	o.	–

(ii) Layer of small herbs	Swampy ground	Drier ground
(*a*) Society of green flowering herbs		
Calyptrocarya glomerulata (Brongn.)	l.f.	–
Dieffenbachia paludicola N. E. Br.	v.r.	–
Diplasia karatifolia L. C. Rich.	–	r.
Erythrodes aratanhensis (Rodr.)	–	r.
Ichnanthus axillaris (Nees)	l.a.	–
Leandra divaricata (Naud.)	–	v.r.
Monotagma Parkeri (Roscoe)	r.	l.f.—l.a.
Nautilocalyx lacteus Sandwith	–	o.
Pariana radiciflora Sagot *ex* Doell.	f.	f.
Psychotria cuspidata Bredem.	v.r.	–
Rapatea paludosa Aubl.	o.	o.—r.
[Unidentified]	r.	r.
(*b*) Society of saprophytes not represented on plot		
(*c*) Society of ferns		
Adiantum hirtum Splitg.	–	r.
A. terminatum Kze.	v.r.	v.r.
Cyclodium meniscoides (Willd.)	v.r.	o.
Danaea simplicifolia Rudge	–	v.r.
Dryopteris funesta (Kze.)	–	v.r.
Nephrolepis rivularis (Vahl)	–	r.
Selaginella Parkeri (Hook. et Grev.)	v.r.	r.
Trichomanes pennatum Klf.	–	r.

Table III. *Sample Plot II. Morabukea consociation.*

N.B. On this plot all trees over 15 ft. high were counted over the *whole* area.

I. Trees over 15 ft. (4·6 m.) high (on whole plot, 400 × 400 ft. [122 × 122 m.]).

Vernacular name	Species	Diameter class						Total number of individuals over	
		Under 4 in. (10 cm.)	4–8 in. (10–20 cm.)	8–12 in. (20–31 cm.)	12–16 in. (31–41 cm.)	16–24 in. (41–61 cm.)	24 in. (61 cm.) and over	15 ft. (4·6 m.) high	4 in. (10 cm.) diam.
Adebero	Paypayrola longifolia Tul.	106	4	–	–	–	–	110	4
Aiamorakushi	Pouteria cladantha Sandwith	6	6	2	–	–	–	14	8
Akarako	Marlierea Schomburgkiana Berg	3	1	–	–	–	–	4	1
Arara	Unonopsis glaucopetala R. E. Fries	[4]*	[3]	–	–	–	–	7	[3]
		7							
Arumatta	Clathrotropis brachypetala (Tul.)	25	4	–	–	1	–	30	5
Assashi	Rheedia Benthamiana Pl. et Tr.	2	1	–	–	–	–	3	1
Assipoko	Pouteria demerarae Sandwith (and other species?)	7	4	1	1	–	–	13	6
Assipokoballi, "Broad Leaf"	? P. Jenmanii (Pittier)	1	1	–	–	–	–	2	1
Assipokoballi, "Fine Leaf"	[Sapotaceae]	7	4	–	–	1	–	12	5
Awassakuli, "Large Leaf"	Tovomita obovata Engler	1	–	–	–	–	–	1	–
Awassakuli, "Small Leaf"	Tovomita or Clusia sp.	1	1	–	–	–	–	2	1
[Bahurada, Hill]	Parinari parvifolia Sandwith	2	–	–	–	–	–	2	–
Baniaballi	Eugenia Arawakorum Sandwith (and allied species?)	5	1	2	–	–	–	8	3
Baradan	[Lauraceae]	–	–	1	–	–	–	1	1
Barataballi	[Sapotaceae]	1	1	1	–	–	–	3	2
Baromalli	Catostemma commune Sandwith	24	20	1	–	1	1	47	23
Dalli	Virola surinamensis (Rol. ex Rottb.)	1	–	–	1	–	–	2	1
[Determa]	Ocotea rubra Mez.	–	1	1	–	–	–	2	2
Duka (= Waramia)	Tapirira Marchandii Engler	3	1	–	1	1	–	6	3
Dukali	—	1	1	–	–	–	–	2	1
Duru	Apeiba Petoumo Aubl.	2	1	–	–	–	–	3	1
Fukadi, "Broad Leaved"	Terminalia Tanibouca Rich.	1	–	–	–	–	–	1	–
Futui	Jacaranda Copaia (Aubl.)	[4]*	[3]	[1]	[–]	1	–	9	[5]
		7		1					
[Greenheart]	Ocotea Rodioei (Schomb.)	13	2	3	5	3	5	31	18
Hachiballi	—	–	1	–	–	–	–	1	1
Haiowa	—	1	–	–	–	–	–	1	–
Haiowaballi	—	3	3	–	–	–	–	6	3
Hakiaballi	? Tabebuia sp.	2	–	–	–	–	–	2	–
Hubudi	[Anacardiaceae]	–	–	–	–	–	1	1	1

Hurуassa	Pithecellobium Jupunba (Willd.)	–	–	–	–	1	–	1	1
Huruereroko	Cordia nodosa Lam.	3	–	–	–	–	–	3	–
Itarra	[Melastomaceae?]	1	–	–	–	–	–	1	–
Ituri-ishi-lukudu	—	8	2	–	–	–	–	10	2
Kabukalli	Goupia glabra Aubl.	8	6	1	–	1	–	16	8
Kaiarima	Maytenus myrsinoides Reiss	4	–	–	–	–	–	4	–
Kairiballi	Licania heteromorpha Bth. var. perplexans Sandwith	7	2	3	–	–	–	12	5
Kakaralli, "Common Black"	Eschweilera Sagotiana Miers	18	18	6	5	5	–	52	34
Kakaralli, "Fine Leaved"	E. Wachenheimii (R. Benoist)	16	5	5	1	–	–	27	11
Kakaralli, "Smooth Leaved"	E. decolorans Sandwith E. pallida Miers	9	4	11	10	–	–	34	25
Kamakutti	Bombax surinamense Uitt.	–	1	–	–	–	–	1	1
Kanoaballi	Byrsonima rugosa Bth.	–	1	–	–	–	–	1	1
Karahoro	Didymopanax Morototoni (Aubl.)	1	2	1	1	–	–	5	4
Karoto, "White"	?Inga rubiginosa (Rich.)	2	–	1	–	–	–	3	1
Kauta	Licania laxiflora Fritsch	7	6	1	1	1	–	16	9
Kautaballi	L. venosa Rusby	19	5	5	4	2	–	35	16
Keriti	[Lauraceae]	3	–	–	–	–	–	3	–
Kokeritiballi	[A name including species of several genera of Sapotaceae]	6	–	2	1	–	–	9	3
Kudibiushi	Sapotaceae	–	–	1	–	–	–	1	1
Kulashiri, "Large Black"	Trichilia Schomburgkii C.DC.	18	3	1	–	–	–	22	4
Kulashiri, "Small Black"	Casearia javitensis H.B.K.	5	2	–	–	–	–	7	2
Kulashiri, "White"	—	1	–	–	–	–	–	1	–
Kumaramara, "Small"	Duroia sp.?	1	–	–	–	–	–	1	–
Kurihikoyoko	Anaxagorea dolichocarpa Sprague et Sandwith	6	–	–	–	–	–	6	–
Kurokai	[Protium decandrum (Aubl.)]	12	6	–	–	–	–	18	6
Kuyama	?Guatteria atra Sandwith	1	–	–	–	–	–	1	–
Mabwa	—	1	–	–	–	–	–	1	–
Maho (both kinds)	Sterculia rugosa R.Br.] S. pruriens (Aubl.)	10	–	5	–	–	–	15	5
Makarasali	Heisteria cauliflora Sm.	1	–	–	–	–	–	1	–
Mamuriballi	—	6	1	1	–	–	–	8	2
Manariballi, "Black"	[Leguminosae]	–	–	–	–	–	1	1	1
Manniballi	Moronobea coccinea Aubl.	6	–	3	1	2	1	13	7
Marishiballi	Licania densiflora Kleinh.	12	–	–	–	–	–	12	–
Moraballi	Pouteria minutiflora (Britton)	7	1	–	–	–	–	8	1
Morabukea	Mora Gonggrijpii (Kleinh.)	318	39	17	9	38	16	437	119
Okokonshi, "Broad Leaf"	Quiina indigofera Sandwith	6	3	4	–	–	–	13	7
Okokonshi, "Fine Leaf"*	Q. guianensis Aubl.	[7]*	[7]	–	–	–	–	14	[7]*
		14							

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* The figures given in brackets represent an arbitrary distribution between the two diameter classes, the two not having been distinguished in the

Table III (*contd.*).

Vernacular name	Species	Diameter class						Total number of individuals over	
		Under 4 in. (10 cm.)	4–8 in. (10–20 cm.)	8–12 in. (20–31 cm.)	12–16 in. (31–41 cm.)	16–24 in. (41–61 cm.)	24 in. (61 cm.) and over	15 ft. (4·6 m.) high	4 in. (10 cm.) diam.
Saramakushi	[Sapotaceae]	–	–	1	1	–	–	2	2
Serebedan	Swartzia sp.	–	–	1	–	–	–	1	1
Shibadan	? Casearia singularis Eichl.	1	1	–	–	1	–	3	2
Shirabulibali	Sloanea amplifrons Johnston	1	–	–	–	–	–	1	–
Silverballi, "Ginger Gale"	[Lauraceae]	2	–	–	–	–	–	2	–
Silverballi, "White"	[Lauraceae]	2	–	–	–	–	–	2	–
Silverballi, "White (Narrow Leaved)"	[Lauraceae]	1	–	1	–	–	–	2	1
["Table Tree"]	Cordia melanoneura Klotzsch	2	6	2	–	–	–	10	8
[Trysil]	Pentaclethra macroloba (Willd.)	20	10	7	3	1	–	41	21
Ulu	? Trattinickia demerarae Sandwith	1	–	–	–	–	1	2	1
Waiaballi	—	5	2	–	–	–	–	7	2
Wallaba, "Soft"	Eperua falcata Aubl.	5	4	4	–	1	–	14	9
Warakusa	Inga spp.	2	1	–	–	1	–	4	2
Warunanna	Hortia regia Sandwith	1	–	–	–	–	–	1	–
Yarri-yarri, "Broad Leaf"	Duguetia pycnastera Sandwith	1	–	–	–	–	–	1	–
Yarri-yarri, "Fine Leaf"	D. neglecta Sandwith	1	–	–	–	–	–	1	–
Yaruru	Aspidosperma excelsum Bth.	3	1	1	–	–	1	6	3
[Unknown, "A"]	Sandwithia guyanensis Lanjouw	91	1	–	–	–	–	92	1
[Unknown, "B"]	—	14	–	–	–	–	–	14	0
[Unknown, "D"]	Mabea Piriri Aubl.	[10]*	[9]	–	–	–	–	19	[9]
		19							
[Unknown, "F"]	—	4	6	3	–	–	–	13	9
[Unknown]	Rinorea Riana (DC.)	1	–	–	–	–	–	1	–
[Unknown]	Tapura guianensis Aubl.	2	–	–	–	–	–	2	–
[Unknown]	—	2	–	–	–	–	–	2	–
[Unknown]	—	–	–	1	1	–	–	2	2
[Unknown]	—	–	–	1	–	–	–	1	1
[Unknown]	[Rosaceae]	1	–	–	–	–	–	1	–
[Unknown]	[Myristicaceae?]	–	1	–	–	–	–	1	1
[Unknown]	—	3	1	–	–	–	–	4	1
[Unknown]	[3 or 4 species]	20	1	–	–	–	–	21	1
	Totals	952	222	103	46	62	27	1412	460
	Total number of trees over 16 in. (41 cm.) diameter							89	

Vernacular name	Species	No. of individuals
Palms: Dallibanna	?Geonoma robusta Burret	4
Lu	—	4
Turu	Jessenia oligocarpa Griseb. et H. Wendl	5
Urishi	—	1
	Total	14

II. Plants under 15 ft. (4·6 m.) high (omitting young trees and bush-ropes).

(i) Layer of shrubs and tall herbs	
Alsophila rostrata (H.B.K.)	r.†
Anaxagorea dolichocarpa Sprague et Sandwith	o.?
Bactris oligoclada Burret	o.
Calathea zingiberina Koern.	r.
Cephaelis violacea (Aubl.)	r.
Cordia nodosa Lam.	v.r.
Diplasia karatifolia L. C. Rich.	l.f.
Duguetia neglecta Sandwith and or D. pycnastera Sandwith	v.r.?
D. Yeshidan Sandwith	o.—f.
Geonoma paniculigera Mart.	o.
Heisteria cauliflora Sm.	v.r.?
Heliconia Ballia L. C. Rich.	r.†
Hemitelia strigosa (J.Sm.)	r.
Ischnosiphon Arouma (Aubl.)	o.
I. gracilis (Rudge)	r.
Naletonia violacea (Aubl.)	v.r.
Paypayrola longifolia Tul.	f.
Psychotria flexuosa Willd.	o.
Renealmia orinocensis Rusby	r.
(ii) Layer of small herbs	
(*a*) Society of green flowering herbs	
Calyptrocarya angustifolia Nees	r.
Cephaelis purpurea (Aubl.)	o.—f.
C. callithrix Miq.	r.
Clidemia conglomerata (Rich.)	l.f.
Ichnanthus panicoides Beauv.	r.—o.
Leandra divaricata (Naud.)	r.
Nautilocalyx lacteus Sandwith	r.
[Unidentified, about 3 species]	o.
(*b*) Society of saprophytes	
Cymbocarpa saccata Sandwith	l.f.
Gymnosiphon sp.	r.
Leiphaimos corymbosa (Splitg.)	r.—o.
Miersiella aristata Sandwith	l.f.
Schizaea fluminensis Miers	l.f.
Voyria rhodochroa Sandwith	v.r.
Voyriella parviflora Miq.	v.r.
(*c*) Society of ferns, etc.	
Adiantum hirtum Splitg.	o.
A. terminatum Kze.	r.
Cyclodium meniscoides (Willd.)	r.
Danaea elliptica Sm.	r.
Lindsaya falcata Dryand.	o.
D. simplicifolia Rudge	r.
Dryopteris funesta (Kze.)	o.
Selaginella Parkeri (Hook. et Grev.)	r.
Trichomanes botryoides Klf. and/or T. diversifrons (Bory)	r.
T. pennatum Klf.	o.

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* The figures given in brackets represent an arbitrary distribution between the two diameter classes, the two not having been distinguished in the field notes.

† =Confined to openings made by fallen trees.

Table IV. *Sample Plot III. Mixed Forest association.*

I. Trees over 4 in. (10 cm.) diameter (on whole plot, 400 × 400 ft. [122 × 122 m.]).

Vernacular name	Species	Diameter class					Total number of individuals over 4 in. (10 cm.) diam.
		4–8 in. (10–20 cm.)	8–12 in. (20–31 cm.)	12–16 in. (31–41 cm.)	16–24 in. (41–61 cm.)	24 in. (61 cm.) and over	
Adebero	Paypayrola longifolia Tul.	1	–	–	–	–	1
Aiamorakushi	Pouteria cladantha Sandwith	4	2	–	–	–	6
Akarako	Marlierea Schomburgkiana Berg	1	–	–	–	–	1
Arara	Unonopsis glaucopetala R. E. Fries	19	3	–	–	–	22
Aruadan	—	1	1	–	1	–	3
Arumatta	Clathrotropis brachypetala (Tul.)	1	2	–	–	–	3
Assashi	Rheedia Benthamiana Pl. et Tr.	2	–	–	–	–	2
Assipoko	Pouteria demerarae Sandwith (and other species?)	3	–	2	3	1	9
Assipokoballi, "Broad Leaf"	? P. Jenmanii (Pittier)	2	1	–	–	–	3
Assipokoballi, "Fine Leaf"	[Sapotaceae]	–	1	–	1	–	2
Awassakuli, "Large Leaf"	Tovomita obovata Engler	1	–	–	–	–	1
Baniaballi	? Eugenia Arawakorum Sandwith	2	2	1	–	–	5
Barabara	Lissocarpa guianensis Gleason	2	–	–	–	–	2
Baradan	—	–	–	–	2	1	3
Baromalli	Catostemma commune Sandwith	8	3	1	1	–	13
[Congo Pump]	Cecropia sp.	1	–	–	–	–	1
Duka (=Waramia)	Tapirira Marchandii Engler	1	1	–	–	–	2
Duru	Apeiba Petoumo Aubl.	5	2	–	1	–	8
Fukadi, "Broad Leaved"	Terminalia Tanibouca Rich.	1	–	1	2	–	4
Futui	Jacaranda Copaia (Aubl.)	1	1	–	–	–	2
[Greenheart]	Ocotea Rodioei (Schomb.)	8	2	5	10	3	28
Hachiballi	—	–	2	–	–	–	2
Ituri-ishi-lukudu	—	1	–	–	–	–	1
Kaiarima	Maytenus myrsinoides Reiss.	2	1	1	1	–	5
Kairiballi	Licania heteromorpha Bth. var. perplexans Sandwith	29	12	–	–	–	41

Kakaralli, "Common Black"	Eschweilera Sagotiana Miers	5	6	14	13	1	39
Kakaralli, "Fine Leaved"	E. Wachenheimii (R. Benoist)	2	–	–	–	–	2
Kakaralli, "Smooth Leaved"	{ Eschweilera decolorans Sandwith E. pallida Miers } (probably mainly the former)	19	14	7	1	1	42
Kanoaballi	Byrsonima rugosa Bth.	–	–	2	–	–	2
Karahoro	Didymopanax Morototoni (Aubl.)	2	–	–	–	–	2
Kauta	Licania laxiflora Fritsch	18	13	5	6	–	42
Kautaballi	L. venosa Rusby	26	16	9	10	–	61
Kirikowa	Iryanthera paraensis Hub.	8	2	–	–	–	10
Kulashiri, "Red"	Matayba opaca Radlk.	1	–	–	–	–	1
Kulashiri, "Large Black"	Trichilia Schomburgkii C.DC.	1	–	–	–	–	1
Kumaramara, "Small"	Duroia sp.?	1	–	–	–	–	1
Kunoko	Licania heteromorpha Bth.	1	–	–	–	–	1
Kurokai	[Protium decandrum (Aubl.)]	4	1	–	–	–	5
Kuyama, "Black"	Guatteria atra Sandwith	–	3	–	–	–	3
[Locust (Simiri)]	[Hymenaea Courbaril L.]	–	–	–	1	–	1
Maho, "Broad Leaved"	[Sterculia rugosa R.Br.]	1	2	1	1	–	5
Maho, "Fine Leaved"	S. pruriens (Aubl.)	8	5	1	–	–	14
Mamuriballi	—	1	1	1	1	–	4
Manniballi	Moronobea coccinea Aubl.	3	1	3	5	–	12
Marishiballi	Licania densiflora Kleinh.	7	–	–	–	–	7
[Monkey Pot] or Wadaduri	Lecythis Davisii Sandwith	–	1	–	–	–	1
Moraballi	Pouteria minutiflora (Britton)	4	1	–	1	–	6
Morabukea	Mora Gonggrijpii (Kleinh.)	–	–	–	1	–	1
Moroinereru	—	1	–	–	–	–	1
Okokonshi, "Broad Leaf"	Quiina indigofera Sandwith	5	3	1	–	–	9
Okokonshi, "Fine Leaf"	Q. guianensis Aubl.	1	–	–	–	–	1
Saramakushi	—	1	2	1	–	–	4
[Sawarri]	[Caryocar nuciferum L.]	–	–	–	2	–	2
Serebedan	Swartzia sp.?	–	1	–	–	–	1
Shibadan	?Casearia singularis Eichl.	1	1	–	1	–	3
Shiballidanni	Hebepetalum humiriifolium (Planch.)	1	–	–	–	–	1
Shirua	—	1	2	–	–	–	3
Silverballi, "Brown"	Nectandra sp.?	–	1	–	1	–	2
Silverballi, "Ginger Gale"	Ocotea sp.	3	–	–	–	–	3
Silverballi, "Kurahara	[Lauraceae]	–	1	1	2	–	4
Silverballi, "White"	[Lauraceae]	2	–	–	–	–	2

Table IV (*contd.*).

Vernacular name	Species	Diameter class					Total number of individuals over 4 in. (10 cm.) diam.
		4–8 in. (10–20 cm.)	8–12 in. (20–31 cm.)	12–16 in. (31–41 cm.)	16–24 in. (41–61 cm.)	24 in. (61 cm.) and over	
Silverballi, "White (red-skin)"	[Lauraceae]	1	–	–	–	–	1
Silverballi, "Yellow"	[Lauraceae]	5	1	–	1	–	7
[Table Tree]	Cordia melanoneura Klotzsch	4	17	4	–	–	25
Tibukushi	[Euphorbiaceae]	–	1	–	–	–	1
[Trysil]	Pentaclethra macroloba (Willd.)	31	20	16	6	–	73
Wadara	Couratari pulchra Sandwith	–	1	–	–	1	2
Wallaba, "Soft"	Eperua falcata Aubl.	6	–	–	1	–	7
Warakusa	Inga spp.	5	2	–	1	–	8
Weshiraure	Xylopia Benthami R. E. Fries	–	1	–	–	–	1
Yarri-yarri	Duguetia neglecta Sandwith and/or D. pycnastera Sandwith	2	–	–	–	–	2
Yaruru	Aspidosperma excelsum Bth.	3	3	2	1	1	10
Yawarridan	Sclerolobium guianense Bth.	3	–	–	–	–	3
[Unknown, "A"]	Sandwithia guyanensis Lanjouw	11	–	–	–	–	11
[Unknown, "D"]	Mabea Piriri Aubl.	5	–	–	–	–	5
[Unknown (like Suradan)]	[Euphorbiaceae?]	2	–	–	–	–	2
[Unknown]	—	1	–	–	–	–	1
[Unknown]	Eugenia essequiboensis Sandwith	–	–	–	2	–	2
[Unknown]	—	–	–	–	1	–	1
[Unknown]	About 10 species	11	1	1	–	–	13
	Totals	314	160	80	81	9	644
	Total number of trees over 16 in. (41 cm.) diameter						90

Palms			
Palms: Dallibanna	?Geonoma robusta Burret	Diameters not estimated	4
Lu	—		2
Turu	Jessenia oligocarpa Griseb. et H. Wendl		4
Urishi	—		1
		Total	11

II. **Trees under 4 in. (10 cm.) diameter and over 15 ft. (4·6 m.) high (on two strips each 25 × 400 ft. [7·6 × 122 m.]).**

Vernacular name	Species	No. of individuals
Adebero	Paypayrola longifolia Tul.	9
Arara	Unonopsis glaucopetala R. E. Fries	4
Arumatta	Clathrotropis brachypetala (Tul.)	1
Assipoko	? Pouteria demerarae Sandwith	1
Assipokoballi, "Broad Leaf"	? P. Jenmanii (Pittier)	2
Baniaballi	? Eugenia Arawakorum Sandwith	3
Baromalli	Catostemma commune Sandwith	4
Buri	Tabernaemontana undulata Vahl	6
Duka (=Waramia)	Tapirira Marchandii Engler	2
[Greenheart]	Ocotea Rodioei (Schomb.)	2
Kabukalli	Goupia glabra Aubl.	1
Kaiarima	Maytenus myrsinoides Reiss	2
Kairiballi	Licania heteromorpha Bth. var. perplexans Sandwith	22
Kakaralli, "Common Black"	Eschweilera Sagotiana Miers	6
Kakaralli, "Smooth Leaved"	E. decolorans Sandwith E. pallida Miers (probably mainly the former)	16
Kauta	L. laxiflora Fritsch	3
Kautaballi	L. venosa Rusby	16
Kirikowa	Iryanthera paraensis Hub.	2
Kunoko	Licania heteromorpha Bth.	1
Kurihikoyoko	Anaxagorea dolichocarpa Sprague et Sandwith	6
Kurokai	[Protium decandrum (Aubl.)]	4
Maho, "Broad Leaved"	[Sterculia rugosa R.Br.]	1
Maho, "Fine Leaved"	S. pruriens (Aubl.)	1
Mamuriballi	—	1
Manniballi	Moronobea coccinea Aubl.	2
Marishiballi	Licania densiflora Kleinh.	3
[Monkey Pot] or Wadaduri	Lecythis Davisii Sandwith	1
Moraballi	Pouteria minutiflora (Britton)	1
Morabukea	Mora Gonggrijpii (Kleinh.)	4
Okokonshi, "Broad Leaf"	Quiina indigofera Sandwith	1
Okokonshi, "Fine Leaf"	Q. guianensis Aubl.	11
Shibadan	? Casearia singularis Eichl.	1
Shirua	[Lauraceae]	1
Silverballi, "Ginger Gale"	[Lauraceae]	2
Silverballi. Kurahara	[Lauraceae]	1
[Trysil]	Pentaclethra macroloba (Willd.)	10

Table IV (*contd.*).

Vernacular name	Species	No. of individuals
Ulu	? Trattinickia demerarae Sandwith	1
Warahaia	—	1
Warakusa	Inga spp.	4
Yarri-yarri, "Fine Leaf"	Duguetia neglecta Sandwith	12
Yaruru	Aspidosperma excelsum Bth.	1
Yawarridan	Sclerolobium guianense Bth.	1
[Unknown, "A"]	Sandwithia guyanensis Lanjouw	29
[Unknown (like Suradan)]	[Euphorbiaceae?]	3
[Unknown]	—	1
[Unknown]	Several species	9
	Total	216

III. Plants under 15 ft. (4·6 m.) high (omitting young trees and bush-ropes).

(i) Layer of shrubs and tall herbs	
Aciotis purpurascens (Aubl.)	v.r.
Alsophila rostrata (H.B.K.)	o.
Anaxagorea dolichocarpa Sprague et Sandwith	o
Bactris oligoclada Burret	o.
Bactris sp. (not flowering)	v.r.
? Calathea zingiberina Koern. (not flowering)	r.
Cephaelis violacea (Aubl.)	o.—f.
Clidemia conglomerata (Rich.)	o.
Cordia nodosa Lam.	r.—o.
Duguetia neglecta Sandwith	a.
D. Yeshidan Sandwith	f.
Hemitelia strigosa (J.Sm.)	o.
Ischnosiphon Arouma (Aubl.)	r.
I. foliosus Gleason	o.
I. gracilis (Rudge)	o.
I. surinamensis (Miq.)	r.
[Scitamineae] (not flowering)	v.r.
Miconia Plukenetii Naud.	r.
Miconia sp.?	r.
Miconia sp.?	v.r.
Paypayrola longifolia Tul.	o.
Tabernaemontana undulata Vahl	f.

(ii) Layer of small herbs	
(*a*) Society of green flowering herbs	
Calyptrocarya angustifolia Nees	v.r.
Cephaelis callithrix Miq.	v.r.
C. purpurea (Aubl.)	v.r.
Ichnanthus panicoides P. Beauv.	r.
[Gramineae]	v.r.
Mapanea macrophylla (Boeck.) or Diplasia karatifolia L. C. Rich. (not flowering)	v.r.
Nautilocalyx lacteus Sandwith	r.—l.f.
? Spathanthus unilateralis (Rudge) (not flowering)	v.r.
(*b*) Society of saprophytes	
Leiphaimos corymbosa (Splitg.)	v.r.
L. tenella (Hook.)	v.r.
(*c*) Society of ferns	
Adiantum hirtum Splitg.	o.
A. terminatum Kze.	r.
Cyclodium meniscoides (Willd.)	o.
Dryopteris funesta (Kze.)	r.—o.
Lindsaya falcata Dryand.?	v.r.
L. nitidissima Rich.	r.
Selaginella Parkeri (Hook. et Grev.)	v.r.
? Trichomanes diversifrons (Bory)	v.r.
T. pennatum Klf.	r.

Table V. *Sample Plot IV. Greenheart consociation.*

I. Trees over 4 in. (10 cm.) diameter (on two plots, together of the same area as the other sample plots, viz. 400 × 400 ft. [122 × 122 m.]).

Vernacular name	Species	Diameter class					Total number of individuals over 4 in. (10 cm.) diam.
		4–8 in. (10–20 cm.)	8–12 in. (20–31 cm.)	12–16 in. (31–41 cm.)	16–24 in. (41–61 cm.)	24 in. (61 cm.) and over	
Adebero	Paypayrola longifolia Tul.	16	–	–	–	–	16
Aiamorakushi	Pouteria cladantha Sandwith	6	2	1	–	–	9
Akarako	Marlierea Schomburgkiana Berg	5	–	–	–	–	5
Arara	Unonopsis glaucopetala R. E. Fries	13	5	–	–	–	18
Aruadan	—	1	3	–	1	–	5
Arumatta	Clathrotropis brachypetala (Tul.)	4	1	–	–	–	5
Assashi	Rheedia Benthamiana Pl. et Tr.	3	–	–	–	–	3
Assipoko	Pouteria demerarae Sandwith (and other species?)	2	1	–	1	–	4
Assipokoballi, "Broad Leaf"	? P. Jenmanii (Pittier)	3	2	1	–	–	6
Assipokoballi, "Fine Leaf"	[Sapotaceae]	–	–	–	1	–	1
Assipokoballi (of Wallaba Forest)	[Sapotaceae]	1	3	1	1	–	6
[Bahurada, Hill]	Parinari parvifolia Sandwith	–	–	1	1	–	2
Baniaballi	? Eugenia Arawakorum Sandwith	1	1	4	–	–	6
Barabara	Lissocarpa guianensis Gleason	6	–	–	–	–	6
Baradan	[Lauraceae]	1	–	–	–	2	3
Baratabballi	[Sapotaceae]	1	3	–	–	–	4
Baromalli	Catostemma commune Sandwith	12	1	3	3	–	19
Baromalli (of Wallaba Forest)	C. fragrans Bth.	4	–	–	–	–	4
Bukobukotokon	Hirtella manigera Kleinh. or allied species	1	–	–	–	–	1
[Determa]	Ocotea rubra Mez.	2	1	–	3	–	6
Dukuria?	—	1	–	–	–	–	1
Duru	Apeiba Petoumo Aubl.	6	3	–	–	–	9
Fukadi, "Broad Leaved"	Terminalia Tanibouca Rich.	–	–	–	–	1	1
Fukadi, "Small Leaved"	Terminalia sp.	–	–	–	1	1	2
Futui	Jacaranda Copaia (Aubl.)	5	1	–	–	–	6
[Greenheart]	Ocotea Rodioei (Schomb.)	2	5	10	38	18	73
Hachiballi	—	–	1	–	–	–	1

Table V (*contd.*).

Vernacular name	Species	Diameter class 4–8 in. (10–20 cm.)	8–12 in. (20–31 cm.)	12–16 in. (31–41 cm.)	16–24 in. (41–61 cm.)	24 in. (61 cm.) and over	Total number of individuals over 4 in. (10 cm.) diam.
Haiariballi, "Black Heart"	[Leguminosae]	1	2	–	–	–	3
Haiowa	—	–	1	–	–	–	1
Hubudiballi	—	1	–	–	–	–	1
Huruassa	Pithecellobium Jupunba (Willd.)	–	–	–	–	1	1
Itarra	[Melastomaceae?]	–	–	1	–	–	1
Ituri-Ishi-Lukudu	—	1	–	–	–	–	1
Kabukalli	Goupia glabra Aubl.	1	–	–	1	–	2
Kairiballi	Licania heteromorpha Bth. var. perplexans Sandwith	26	14	1	–	–	41
Kakaralli, "Common Black"	Eschweilera Sagotiana Miers	34	9	7	8	1	59
Kakaralli, "Fine Leaved Black"	E. Wachenheimii (R. Benoist)	26	3	4	–	–	33
Kakaralli, "Smooth Leaved"	{E. decolorans Sandwith E. pallida Miers}	16	12	8	1	–	37
Kanoaballi	Byrsonima rugosa Bth.	–	–	–	1	–	1
Karahoro	Didymopanax Morototoni (Aubl.)	–	–	–	1	–	1
Kauta	Licania laxiflora Fritsch	2	4	1	–	–	7
Kautaballi	L. venosa Rusby	12	7	14	10	–	43
Keriti	—	1	–	–	–	–	1
Kibihidan	—	–	1		–	–	1
Kirikowa	Iryanthera paraensis Hub.	–	1	–	–	–	1
Kudibiushi	—	2	–	–	1	–	3
Kulashiri, "Small Black"	Casearia javitensis H.B.K.	2	–	–	–	–	2
Kulashiri, "Red Fine Leaf"	—	2	1	–	–	–	3
Kurokai	[Protium decandrum (Aubl.)]	7	4	–	–	–	11
Kuyama, "Black"	Guatteria atra Sandwith	–	2	–	–	–	2
Kuyama, "White"	Xylopia cinerea Sandwith	1	–	–	–	–	1
[Locust]	[Hymenaea Courbaril L.]	1	–	–	–	–	1
Maho, "Broad Leaved"	[Sterculia rugosa R.Br.]	3	3	1	2	–	9
Maho, "Fine Leaved"	S. pruriens (Aubl.)	5	–	3	2	–	10
Mamuriballi	—	3	–	1	–	–	4
Manniballi	Moronobea coccinea Aubl.	5	1	–	4	3	13

Marishiballi	Licania densiflora Kleinh. (or perhaps L. buxifolia Sandwith)	1	–	–	1	–	2
[Monkey Pot] or Wadaduri	Lecythis Davisii Sandwith	2	–	–	–	–	2
Mora	Mora excelsa Bth.	1	–	1	1	1	4
Moraballi	Pouteria minutiflora (Britton)	1	–	–	–	–	1
Okokonshi, "Broad Leaf"	Quiina indigofera Sandwith	14	10	8	–	–	32
Okokonshi, "Fine Leaf"	Q. guianensis Aubl.	1	–	–	–	–	1
Sada	—	4	2	1	2	–	9
[Sawarri]	[Caryocar nuciferum L.]	–	–	–	1	1	2
Serebedan	Swartzia sp.?	1	3	–	–	–	4
Shibadan	?Casearia singularis Eichl.	3	–	–	–	–	3
Shirada	Inga sp.?	–	–	–	1	–	1
Shirabuliballi	Sloanea amplifrons Johnston	1	–	–	–	–	1
Shirua	—	1	–	–	–	–	1
Silverballi, "Brown"	Nectandra sp.?	1	–	1	–	–	2
Silverballi, "Greenheart Gale"	Ocotea sp.?	2	–	1	–	–	3
Silverballi, "Ginger Gale"	[Lauraceae]	3	–	–	–	–	3
Silverballi, Kurahara	[Lauraceae]	2	–	–	1	–	3
Silverballi, "White, Red-skin"	[Lauraceae]	1	–	–	–	–	1
Silverballi, "White"	[Lauraceae]	1	–	–	–	–	1
Silverballi, "Yellow"	[Lauraceae]	1	–	–	–	–	1
"Table Tree"	Cordia melanoneura Klotzsch	4	3	–	–	–	7
Tatabu	[Leguminosae]	–	–	1	–	–	1
[Trysil]	Pentaclethra macroloba (Willd.)	28	28	10	5	–	71
Wallaba, "Soft"	Eperua falcata Aubl.	–	2	1	1	–	4
Waiaballi	—	1	–	–	–	–	1
Warakusa	Inga spp.	2	2	3	–	–	7
Warunanna	Hortia regia Sandwith	2	–	2	–	–	4
Yarri-yarri	{Duguetia neglecta Sandwith and/or D. pycnastera Sandwith}	4	–	–	–	–	4
Yaruru	Aspidosperma excelsum Bth.	6		–	3	1	13
Yawarridan	Sclerolobium guianense Bth.	1	–	–	1	–	2
[Unknown, "A"]	Sandwithia guyanensis Lanjouw	50	2	–	–	–	52
[Unknown, "F"]	[Myrtaceae?]	7	–	1	–	–	8
[Unknown (like Corkwood]	—	–	–	1	1	–	2
[Unknown]	4 species	3	1	–	–	–	4
	Totals	397	154	93	99	30	773
	Total number of trees over 16 in. (41 cm.) diameter						129

Table V (*contd.*).

II. Trees under 4 in. (10 cm.) diameter and over 15 ft. (4·6 m.) high (on two strips each 25 × 400 ft. [7·6 × 122 m.]).

Vernacular name	Species	No. of individuals
Adebero	Paypayrola longifolia Tul.	12
Aiamorakushi	Pouteria cladantha Sandwith	1
Akarako	Marlierea Schomburgkiana Berg	2
Arara	Unonopsis glaucopetala R. E. Fries	3
Assipoko	? Pouteria demerarae Sandwith	2
Assipokoballi, "Broad Leaf"	? P. Jenmanii (Pittier)	1
Assipokoballi, "Fine Leaf"	[Sapotaceae]	1
Baniaballi	? Eugenia Arawakorum Sandwith	1
Baromalli	Catostemma commune Sandwith	2
Buri	Tabernaemontana undulata Vahl	7
Futui	Jacaranda Copaia (Aubl.)	1
[Greenheart]	Ocotea Rodioei (Schomb.)	2
Haiowa	—	1
Haiowaballi	—	1
Hubudiballi	—	2
Ituri-Ishi-Lukudu	—	1
Kairiballi	Licania heteromorpha Bth. var. perplexans Sandwith	10
Kakaralli, "Common Black"	Eschweilera Sagotiana Miers	12
Kakaralli, "Fine Leaved"	E. Wachenheimii (R. Benoist)	13
Kakaralli, "Smooth Leaved"	{E. decolorans Sandwith E. pallida Miers}	6
Kauta	L. laxiflora Fritsch	5
Kautaballi	L. venosa Rusby	9
Kokeritiballi	[A name including species of several genera of Sapotaceae]	2
Kulashiri, "Red, Fine Leaved"	—	3
Kulashiri, "Small Black"	Casearia javitensis H.B.K.	4
Kumaramara, "Large"	Duroia eriopila L. fil.	1
Kunoko	Licania heteromorpha Bth.	2
Kurihikoyoko	Anaxagorea dolichocarpa Sprague et Sandwith	15
Kurokai	[Protium decandrum (Aubl.)]	12
Mano, "Fine Leaved"	Sterculia pruriens (Aubl.)	2
Mamuriballi	—	5
Manniballi	Moronobea coccinea Aubl.	2
[Monkey Pot] or Wadaduri	Lecythis Davisii Sandwith	1
Moraballi	Pouteria minutiflora (Britton)	1

Okokonshi, "Broad Leaf"	Quiina indigofera Sandwith	5
Okokonshi, "Fine Leaf"	Q. guianensis Aubl.	21
Sada	—	1
Serebedan	Swartzia sp.	2
Shibadan	Casearia singularis Eichl.	4
Silverballi, Kurahara	[Lauraceae]	1
Silverballi, "White"	[Lauraceae]	1
Silverballi, "Yellow"	[Lauraceae]	2
[Trysil]	Pentaclethra macroloba (Willd.)	9
Waiaballi	—	2
Yarri-yarri	{Duguetia neglecta Sandwith and/or D. pycnastera Sandwith}	4
[Unknown, "A"]	Sandwithia guyanensis Lanjouw	27
[Unknown, "F"]	—	2
[Unknown]	2 species	3
	Total	229

III. Plants under 15 ft. (4·6 m.) high (omitting young trees and bush-ropes).

(i) Layer of shrubs and tall herbs	
Alsophila rostrata (H.B.K.)	f.—o.
Anaxagorea dolichocarpa Sprague et Sandwith	a.
Bactris oligoclada Burret	f. (young)
Calathea zingiberina Koern.	r.
Cephaelis violacea (Aubl.)	r.—o.
Clidemia conglomerata (Rich.)	o.
Cordia nodosa Lam.	o.
Heliconia Ballia L. C. Rich.	r.
Hemitelia strigosa (J.Sm.)	r.
Ischnosiphon Arouma (Aubl.)	v.r.
I. foliosus Gleason	o.
I. gracilis (Rudge)	v.r.
I. surinamensis (Miq.)	o.
? Jessenia oligocarpa Griseb. et H. Wendl.	f. (young)
Sandwithia guyanensis Lanjouw	r.
Miconia Plukenetii Naud.	v.r.
Paypayrola longifolia Tul.	o.
Tabernaemontana undulata Vahl	—
Tococa aristata Bth.	r.

(ii) Layer of small herbs	
(*a*) Society of green flowering herbs	
Calyptrocarya angustifolia Nees	o.
Centrosolenia densa (C. H. Wright)	l.a.—o.
Cephaelis purpurea (Aubl.)	f.—l.a.
C. callithrix Miq.	o.
Ichnanthus panicoides Beauv.	v.r.
Mapanea macrophylla (Boeck.)	l.f.
Nautilocalyx lacteus Sandwith	r.
Melastomataceae [unidentified]	r.
(*b*) Society of saprophytes	
Gymnosiphon Altsoni Gleason	v.r.
Gymnosiphon (one or two spp.?)	v.r.
Leiphaimos corymbosa (Splitg.)	r.
Schizaea fluminensis Miers	r.
(*c*) Society of ferns	
Cyclodium meniscoides (Willd.)	f.
Dryopteris funesta (Kze.)	r.
Lindsaya nitidissima Rich.	v.r.
Selaginella Parkeri (Hook. et Grev.)	r.
{Trichomanes diversifrons (Bory) (and/or T. botryoides Klf.)}	v.r.
T. pennatum Klf.	r.—o.

Table VI. *Sample Plot V. Wallaba consociation.*

I. Trees over 4 in. (10 cm.) diameter (on whole plot, 400 × 400 ft. [122 × 122 m.]).

Vernacular name	Species	Diameter class 4–8 in. (10–20 cm.)	8–12 in. (20–31 cm.)	12–16 in. (31–41 cm.)	16–24 in. (41–61 cm.)	24 in. (61 cm.) and over	Total number of individuals over 4 in. (10 cm.) diam.
Aiamoradan	Couepia pauciflora Huber	7	–	–	–	–	7
Aiamorakushi	Pouteria cladantha Sandwith	1	–	–	–	–	1
Akarako	Marlierea Schomburgkiana Berg	4	–	–	–	–	4
Arara	Unonopsis glaucopetala R. E. Fries	–	–	1	–	–	1
Assipokoballi, "Fine Leaf" (of Wallaba Forest)	[Sapotaceae]	4	14	2	–	–	20
Assashi	Rheedia Benthamiana Pl. et Tr.	1	–	–	–	–	1
Awassakuli, "Small Leaf"	Tovomita Schomburgkii Pl. et Tr. Clusia Fockeana Miq.	13	1	–	–	–	14
Bania	—	4	1	–	–	–	5
Barabara	Lissocarpa guianensis Gleason	3	1	–	–	–	4
Barataballi	[Sapotaceae?]	7	3	2	–	–	12
Baromalli (of Wallaba Forest)	Catostemma fragrans Bth.	89	39	8	3	–	139
Duka (=Waramia)	Tapirira Marchandii Engler	–	–	1	–	–	1
Duru	Apeiba Petoumo Aubl.	1	2	–	–	–	3
Fukadi, "Small Leaved"	Terminalia sp.	9	4	1	5	–	19
[Greenheart]	Ocotea Rodioei (Schomb.)	1	2	2	2	–	7
Hachiballi	—	10	–	1	–	–	11
Haiariballi	Two species? [Leguminosae]	11	4	7	2	1	25
Hishiruadan	—	2	1	–	–	–	3
Hiwarradan	—	6	4	–	–	–	10
Huruassa	Pithecellobium Jupunba (Willd.)	–	–	1	–	–	1
Immirimiaballi	Cassia pteridophylla Sandwith	18	18	8	1	–	45
Itikibouraballi	Swartzia xanthopetala Sandwith S. Benthamiana Miq.	3	2	3	1	–	9
Kakaralli, Wena (of Wallaba Forest)	Eschweilera corrugata (Poit.)	14	6	6	2	–	28
Kakarwa	[Sapotaceae?]	–	2	–	–	–	2
Kamakutti (of Wallaba Forest)	Bombax flaviflorum Pulle	5	1	–	–	–	6
Kautaballi	Licania venosa Rusby	1	–	–	–	–	1

Korokororo	[Leguminosae]	10	7	7	5	–	29
Kulashiri, "Red"	Matayba opaca Radlk.	6	1	–	–	–	7
Kulashiri, "Small Leaf"	—	3	–	–	–	–	3
Kumaramara, "Large"	Duroia eriopila L. fil.	9	1	–	–	–	10
Kumaramara, "Small"	Duroia sp.?	1	–	–	–	–	1
Kunoko	Licania heteromorpha Bth.	2	3	–	–	–	5
Mabwa	? Plumeria Sucuuba Spruce *ex* Müll. Arg.	2	–	–	–	–	2
Manabadin	—	–	1	–	–	–	1
Mapourokuni	Inga sp. or near	1	–	–	–	–	1
Marishiballi (of Wallaba Forest)	Licania buxifolia Sandwith	72	35	1	4	–	112
Moraballi	Pouteria minutiflora (Britton)	3	2	–	–	–	5
Moroballi	Talisia squarrosa Radlk.	4	5	5	3	–	17
Okokonshi	Quiina guianensis Aubl. or Q. indigofera Sandwith	1	–	–	–	–	1
Pakuri	—	1	1	–	–	–	2
[Purpleheart] or Kuroburelli	Peltogyne pubescens Bth.	1	1	–	–	–	2
Saramakushi	[Sapotaceae?]	–	1	–	–	–	1
Serebedan	Swartzia sp.?	7	6	–	–	–	13
Shibadan	? Casearia singularis Eichl.	1	2	2	1	–	6
Shirada	Inga sp.?	–	–	1	–	–	1
Shirua	[Lauraceae]	2	–	1	–	–	3
Silverballi, "Brown"	Nectandra sp.?	7	2	1	–	–	10
Silverballi, "Yellow"	[Lauraceae]	6	2	3	–	–	11
Tibukushi	[Euphorbiaceae?]	3	1	–	–	–	4
Ulu	? Trattinickia demerarae Sandwith	3	–	–	–	–	3
Waiaballi	[Several species?]	7	–	–	–	–	7
Wallaba, Ituri*	Eperua grandiflora (Aubl.) E. Jenmani Oliv.	7	11	8	1	-	27
Wallaba, "Soft"	E. falcata Aubl.	47	43	37	64	3	194
Warunanna	Hortia regia Sandwith	8	5	1	–	–	14
Yaruru	Aspidosperma excelsum Bth.	7	8	1	1	–	17
Yawarridan	Sclerolobium guianense Bth.	1	–	–	–	–	1
Yekuru	—	8	3	–	–	–	11
[Unknown, "A"]	Sandwithia guyanensis Lanjouw	3	–	–	–	–	3
[Unknown]	—	–	–	–	1	–	1
[Unidentified]	About 12 species	10	3	2	–	–	15
	Totals	457	249	113	96	4	919
	Total number of trees over 16 in. (41 cm.) diameter						100

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* The distinctness of the two species included under this name is somewhat doubtful. (See *Kew Bull. of Misc. Inf.* 1931, p. 366.)

Table VI (*contd.*).

II. Trees under 4 in. (10 cm.) diameter and over 15 ft. (4·6 m.) high (on two strips each 25 × 400 ft. [7·6 × 122 m.]).

Vernacular name	Species	No. of individuals
Aiamoradan	Couepia pauciflora Huber	4
Akarako	Marlierea Schomburgkiana Berg	21
Assashi	Rheedia Benthamiana Pl. et Tr.	1
Assipokoballi, "Fine Leaf" (of Wallaba Forest)	—	5
Awassakuli, "Large Leaf"	Tovomita obovata Engler	1
Awassakuli, "Small Leaf"	T. Schomburgkii Pl. et Tr. Clusia Fockeana Miq.	7
Barata	Ecclinusa psilophylla Sandwith	21
Barataballi	—	7
Baromalli (of Wallaba Forest)	Catostemma fragrans Bth.	40
Bania	—	1
Baniaballi	? Eugenia Arawakorum Sandwith	1
[Greenheart]	Ocotea Rodioei (Schomb.)	2
Hachiballi	—	4
Haiariballi	Two species?	8
Hiwarradan	—	4
Immirimiaballi	Cassia pteridophylla Sandwith	9
Kakaralli, Wena (of Wallaba Forest)	Eschweilera corrugata (Poit.)	3
Kamakutti (of Wallaba Forest)	Bombax flaviflorum Pulle	6
Korokororo	[Leguminosae]	11
Kulashiri, "Large Black"	Trichilia Schomburgkii C.DC.	1
Kulashiri, "Red"	Matayba opaca Radlk.	5
Kulashiri, "Small Black"	Casearia javitensis H.B.K.	2
Kumaramara, "Large"	Duroia eriopila L. fil.	6
Kunoko	Licania heteromorpha Bth.	1
Mabwa	? Plumeria Sucuuba Spruce *ex* Müll. Arg.	2
Marishiballi (of Wallaba Forest)	Licania buxifolia Sandwith	24
Moraballi	Pouteria minutiflora (Britton)	1
Rokoroko	—	1
Serebedan	Swartzia sp.	1
Shibadan, "Large Kind"	—	3
Silverballi, "Brown"	Nectandra sp.?	1
Silverballi, "Yellow"	[Lauraceae]	13
Tibukushi	[Euphorbiaceae]	1
Ulu	? Trattinickia demerarae Sandwith	1

Wallaba, Ituri	Eperua grandiflora (Aubl.) E. Jenmani Oliv.	2
Wallaba, "Soft"	E. falcata Aubl.	10
Waiaballi	Several species?	7
Warunanna	Hortia regia Sandwith	4
Yarri-yarri	Duguetia neglecta Sandwith (and D. pycnastera Sandwith?)	20
Yawarridan	Sclerolobium guianense Bth.	2
Yekuru	—	3
[Unknown, "A"]	Sandwithia guyanensis Lanjouw	7
	Total	284

III. Plants under 15 ft. (4·6 m.) high (omitting young tree and bush-ropes).

(i) Layer of shrubs and tall herbs

Alsophila rostrata (H.B.K.) Mart.	f.—o.
[Bromelia Karatas L.]	—
Bactris oligoclada Burret	o.
Cephaelis dichotoma Rudge	r.
Geonoma robusta Burret	v.r. (young)
Duguetia neglecta Sandwith	f. (mostly immature)
Heliconia Ballia L. C. Rich.	o.
Heliconia sp.?	v.r.
Heisteria cauliflora Sm.	v.r.?
Ischnosiphon foliosus Gleason	o.
I. surinamensis (Miq.)	f.
Ixora Schomburgkiana Bth.	f.
Jessenia oligocarpa Griseb. et H. Wendl.	f. (all young)
Tococa aristata Bth.	o.

(ii) Layer of small herbs

(*a*) Society of green flowering herbs	
Anthurium sp.	v.r.
Centrosolenia densa (C. H. Wright)	a.—o.
?Mapanea macrophylla (Boeck.)	v.r.
Piper moraballianum Trel.	v.r.
Tillandsia sp.?	v.r
Triphora amazonica Schlechter	r.
(*b*) Society of saprophytes	
Leiphaimos aphylla (Jacq.)	r.
L. corymbosa (Splitg.)	v.r.
Schizaea fluminensis Miers	v.r.
(*c*) Society of ferns	
Lindsaya falcata Dryand.	r
L. nitidissima Rich.	r
Trichomanes arbuscula Desv.	—

BOTANY OF THE CAMBRIDGE EXPEDITION TO EDGE ISLAND, S.E. SPITSBERGEN, IN 1927

PART II. THE VEGETATION[1]

BY A. P. G. MICHELMORE, B.A., F.E.S.

(*With Plates XV–XVII and one Figure in the Text.*)

CONTENTS.

PAGE
I. Introduction 156
II. Description of the plant communities 157
III. Geology and soil 164
IV. The topography and the distribution of the plant communities . 165
V. The west coast of Stor Fjord 171
VI. Summerhayes and Elton's climatic zones 172
VII. Plants and soil 174
VIII. Summary 175
References 176

I. INTRODUCTION.

IN the course of the late Mr H. G. Watkins' Cambridge Expedition to Edge Island in 1927 some observations were made on the vegetation. Lists of the species of plants found and of the places visited have been given in the first part of this paper (**3**). The ecological notes made are here presented and correlated with Summerhayes and Elton's work on the ecology and zonation of the vegetation of Spitsbergen (**4**, **5**). Their papers summarise the work of their predecessors so fully that there is no need to refer again to the earlier writers.

It was not found possible to study the Fungi, Lichens or Bryophytes apart from making general notes on their presence or absence. On the flowering plants also the notes were incomplete, because some of the grasses, particularly those of the genus *Poa*, the hairy forms of *Cerastium*, the yellow-flowered species of *Draba* of the *D. alpina* group and a few other plants were not distinguished properly in the field.

The object of the expedition was to explore Edge Island[2], which is the south-eastern of the four main islands forming the Spitsbergen archipelago. We landed also at two places on Barents' Island, the island which lies to the north of Edge Island. The geology and topography of the two islands are similar, and the vegetation at these two places was like that of similar spots in Edge Island. The following account of the vegetation given in Sections II, III and IV of this paper may therefore be taken to hold good for both islands. Visits were also paid to three places on the east coast of West Spitsbergen. The vegetation here was not quite what had been expected after seeing the shores of Edge Island on the opposite coast of Stor Fjord, and these three stations are considered separately in Section V. In Section VI an attempt is made to explain the differences between the two coasts of Stor Fjord, and in Section VII some imperfectly understood observations on soil are mentioned.

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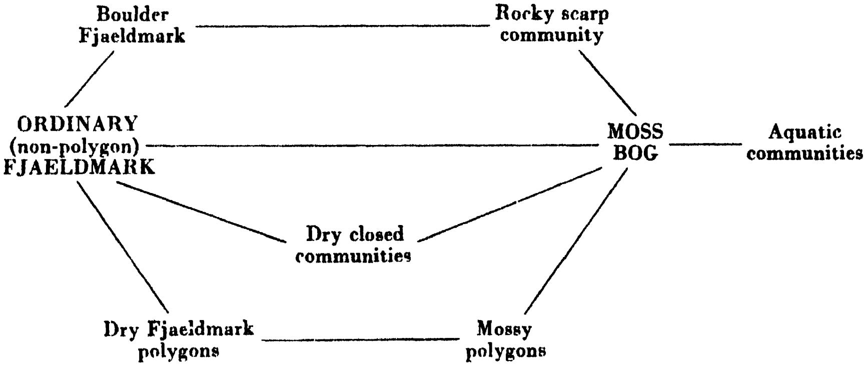
[1] Part I of this paper—"Itinerary and List of Plants"—appeared in the *Kew Bulletin*, No. 1, January, 1934, pp. 30–39.

[2] For an outline map showing Edge Island see folding map opposite p. 193 in (**5**).

The help which I have received from various people in connection with this work has already been gratefully acknowledged in my earlier paper. Here I would record the kindness of Mr Summerhayes and Mr Elton in giving separates, and especially I must acknowledge the inspiration which has been gained from their two joint papers, to which this is such an unworthy supplement. I am much indebted to Mr C. T. Dalgety, ornithologist to the expedition, for the use of some of his photographs to illustrate this paper.

II. DESCRIPTION OF THE PLANT COMMUNITIES.

The vegetation of Edge Island and Barents' Island is very uniform. This is due in part to the uniformity of the geology but more to the rigour of the physical environment, which prevents any but the lowest types of vegetation from developing. All the plants are lowly and herbaceous or else are woody herbs, such as *Salix polaris* Wahlenb. and *Dryas octopetala* L. There are only two important communities, with others which have some of the characteristics of each. The chief one is "fjaeldmark," an open community rich in flowering plants, lichens and mosses. In the local patches where the ground is both moist and stable a quite distinct moss bog develops. This is a closed community dominated by mosses and with some lichens and flowering plants. A few species of the latter are peculiar to the moss bog. The relationships of the other communities described below to the two main ones are shown in the above diagram, in which transitions occur along the lines indicated.



The differences between these communities depend on the state of the substratum. Usually there is direct transition between moss bogs and the surrounding fjaeldmark, but in places peculiar soil conditions cause polygonal cracking or arrangement of pebbles in the ground, and the distribution of the plants is affected. Elsewhere the presence of solid rock alters the vegetation. Occasionally closed communities are to be found on comparatively dry soil, but this is so rare an occurrence that the conditions causing it are evidently purely local and are probably different in the different cases.

Although transitions could be found along the lines shown in the diagram, no evidence was seen of actual change going on from one community to another, except where this was caused by an independent change in soil conditions. In Spitsbergen there is probably little true plant succession, *i.e.* vegetational development, in which the growth of one kind of vegetation gradually alters conditions till they are suitable for the invasion of a new kind. The "successions" described by Summerhayes and Elton (**4**, **5**) and by Walton (**6**) depend on changes due to other causes than the growth of the vegetation itself. Elton (**1**), however, has shown how plants act on the soil in a manner which reacts on their own distribution by causing differential thawing in polygon soils in Spitsbergen. Studies of moss hummocks would also certainly show similar true plant succession on a small scale, but on a large scale it is probably absent.

Besides the communities shown in the diagram there are encrusting lichens in great variety. The presence or absence of these has little effect on the higher plants, and they are not considered in this paper. Here and there little patches of green alga (*Vaucheria* ?) grow under stones and bones. These probably depend on purely local conditions, which are not important in discussing the higher vegetation.

Ordinary Fjaeldmark is the community which occupies most of the land free from ice. It includes all stages between ground with an abundance of isolated plants and a barren waste, where only the closest search can disclose an occasional tiny tuft of moss under a stone. Almost every species of plant found in this part of the country occurs in the fjaeldmark. Only a few bog plants are absent. A single patch often contains quite a variety of flowers, with *Papaver radicatum* Rottb., *Saxifraga* spp. and *Cerastium* spp. making an attractive show. In the richer types of fjaeldmark there are often cushions of moss, which give hospitality to a number of plants, such as *Salix polaris* Wahlenb., *Saxifraga oppositifolia* L. and *Stellaria longipes* Goldie. Drought, which appears to be the usual factor restricting the vegetation to an open or fjaeldmark community, prevents the mosses from being very luxuriant, but *Cladonia rangiferina* Web. and other upright lichens grow well in many places. Plants, such as *Ranunculus sulphureus* Soland., which grow usually in wet places, are absent from the drier types of fjaeldmark and are rather dwarf in the wetter types. The following is a list of the regular fjaeldmark plants from various localities:

Alopecurus alpinus Sm.
Braya purpurascens Bunge
Cardamine bellidifolia L.
C. pratensis L.
Cerastium hyperboreum Tolm.
C. alpinum L.
C. alpinum L. × Regelii Ostenf.
C. Regelii Ostenf.
Cochlearia groenlandica L.
Deschampsia alpina R. et Sch.
Draba alpina L.
D. glacialis Adams
D. lactea Adams
D. oblongata R.Br.
D. subcapitata Simm.
Equisetum variegatum Schleich.
Festuca arenaria Osb.
F. brevifolia R.Br.
Juncus biglumis L.
Luzula confusa Lindeb.
Melandryum apetalum Fenzl.
Minuartia biflora Schinz. et Thell.
M. verna Hiern.
Oxyria digyna Hill
Papaver radicatum Rottb.
Pedicularis hirsuta L.
Phippsia algida R.Br.
Poa alpigena Lindm. × alpina L.
P. alpigena Lindm. × rigens Hartm.
P. rigens Hartm.
Polygonum viviparum L.
Puccinellia angustata R.Br.
P. Vahliana Scribn. et Merr.
Ranunculus pygmaeus Wahlenb.
R. sulphureus Soland.
Sagina intermedia Fenzl.
Salix polaris Wahlenb.
Saxifraga cernua L.
S. comosa Fellm.
S. flagellaris Willd.
S. groenlandica L.
S. hieraciifolia Waldst. et Kit.
S. Hirculus L.
S. nivalis L.
S. oppositifolia L.
S. rivularis L.
S. tenuis H.Sm.
Silene acaulis L.
Stellaria longipes Goldie

In addition the following six species were found once each in fjaeldmark, but they cannot be considered as regular fjaeldmark plants:

Carex ursina Dew.
Dryas octopetala L.
Koenigia islandica L.
Potentilla emarginata Pursh.
P. pulchella R.Br.
Taraxacum arcticum Dahlst.

Carex ursina Dew. and *Koenigia islandica* L. were found nowhere else, so it is not possible to say why they were so local. The other four species are plants found more commonly in other habitats and are dealt with later.

In the richer fjaeldmark areas all the species mentioned in the list above are capable of growing, but in barren places only the hardier plants can live. As far as can be deduced from superficial observation without experiments, water supply and exposure to the weather are the two factors generally controlling the richness of fjaeldmark. Either exposure or drought will produce a similar vegetation, but the component plants are not quite the same. Amongst the first species to disappear, as conditions recede from the optimum, are the following, which live only on fairly damp soil:

Cardamine pratensis L.
Juncus biglumis L.
Ranunculus pygmaeus Wahlenb.
R. sulphureus Soland.
Saxifraga rivularis L.

These are followed by the species given below:

Alopecurus alpinus Sm.
Deschampsia alpina R. et Sch.
Draba lactea Adams
Equisetum variegatum Schleich.
Festuca arenaria Osb.
Melandryum apetalum Fenzl.
Minuartia biflora Schinz. et Thell.
Phippsia algida R.Br.
Saxifraga comosa Fellm.
S. flagellaris Willd.
S. hieraciifolia Waldst. et Kit.
S. Hirculus L.

Some attempt at distinguishing the effects of soil drought and exposure to the elements above ground may be made by noting the optimum humidity for the different species. Besides the five species mentioned in the last list but one, *Alopecurus alpinus* Sm. and *Saxifraga Hirculus* L. of the last list are partial to wet places, and their occurrence is probably limited mainly by drought. The other ten plants named in the last list find the best conditions for growth in ordinary fjaeldmark without excessive moisture. As they live in those places in which most of the hardier and more widely distributed species grow best, it may be suspected that it is largely susceptibility to the weather which prevents their wider spread.

Braya purpurascens Bunge, *Festuca brevifolia* R.Br. and *Silene acaulis* L. also do not grow in the less favourable places, but their distribution is different from that of the plants just mentioned. It appears that the texture or some property of the soil other than water supply determines their occurrence. They are dealt with below in Sections IV and VII.

In the driest fjaeldmark the higher plants are usually restricted to the following species, of which the hardiest are marked with asterisks:

*Cerastium, hairy forms
*C. Regelii Ostenf.
Luzula confusa Lindeb.
Minuartia verna Hiern.
*Papaver radicatum Rottb.
Poa spp.
Polygonum viviparum L.
Sagina intermedia Fenzl.
*Saxifraga cernua L.
S. groenlandica L.
*S. oppositifolia L.
S. tenuis H.Sm.

Where there is enough moisture to support a little moss, *Salix polaris* Wahlenb. and *Stellaria longipes* Goldie also grow. These two plants, especially the former, can stand a severe climate, but their straggling method of growth makes it difficult for them to flourish without support from other plants.

Although the fjaeldmark is in the main an open community, the moss hummocks of the richer types are little subsidiary closed communities. Study of the development of moss hummocks and their invasion by other plants would be interesting.

Another point needing investigation is the possibility that the neighbouring plants of a community which appears open may really be in severe competition owing to their root systems meeting below ground, while their aerial parts are widely separated. The collection of specimens of plants in Spitsbergen soon shows that the roots of most fjaeldmark plants are much longer than their stems. Summerhayes and Elton (**4**, p. 237) have pointed out how sensitive *Saxifraga oppositifolia* L. is to competition. Their observations (**5**, p. 253), which I can confirm, of *Papaver radicatum* Rottb. growing best in barren places, where few other plants can live, may also show the effect of root competition, and do not necessarily mean that this species is actually best suited to an excessively severe climate. A little digging would soon show if there were any truth in this suggestion.

In places where there is no "earth creep" the ordinary fjaeldmark may be replaced by **Dry Fjaeldmark Polygons.** These consist of rounded or roughly polygonal areas of ground outlined, as a rule, by bands of stones tilted up on their edges and 2 or 3 in. across. The polygons seen varied from 1 to 7 ft. in diameter. On gentle slopes the polygons may be elongated in the direction of the slope, but steep slopes have too unstable a surface for any polygon formation. The structure and formation of these polygons, which have quite a literature of their own, do not concern us here. A recent paper on the subject is that by Elton (**1**). Plants grow readily on the stony borders, but the centres are almost always bare, perhaps because of bad soil aeration. The vegetation of the borders is similar to that of the ordinary fjaeldmark. *Papaver radicatum* Rottb. strays on to the polygon centres more often than any other species.

The **Mossy Polygon Community** is a type of community intermediate between the dry polygon and moss bog, and it grades into both. It grows mainly on what Elton (**1**) calls "mud polygons," which have no stone border, but it also grows on wet "stone polygons." The mossy polygons seen were seldom more than 2 ft. across. They occur on wetter ground than the dry polygons. The vegetation differs from that of the dry polygons in being a closed community dominated by mosses like those of the moss bog. The moss forms thick cushions, into which one sinks when walking. The mossy borders are usually broader than the band of vegetation bordering the dry polygons, and the central areas are less stony. The wettest kind of mossy polygon occurs in the form of somewhat convex, round patches of soft mud in the middle of bog. Here the moss border is broader than the small polygon centre itself and is not to be differentiated from the moss bog community in which it occurs. *Ranunculus sulphureus* Soland., *Salix polaris* Wahlenb. and *Saxifraga oppositifolia* L. are typical plants of the mossy polygon community, which has the ordinary fjaeldmark species in diminished numbers and the bog species in the damper parts.

Moss Bog occupies wet ground where the gradient is not steep enough for the water to erode stream channels or wash away plants. Mosses are dominant and form a closed community rather poor in other plants. Small patches of *Sphagnum* occur locally, but this moss never becomes dominant. The wettest parts of the bogs are almost free from flowering plants and lichens, being just flat beds of sodden moss up to 1 ft. or more thick. Below the moss there is always a layer of hard and presumably frozen ground. Where the water-level of the bog is above the moss, brown or green masses of *Nostoc* (?) grow unattached. They dry up when the water-level sinks below them. Various filamentous Green and Blue-Green Algae, often with Diatoms, Flagellates, etc., also grow in such situations. Where the bog is a little drier, the moss is inclined to be hummocky, and the flowering plants grow principally on the hummocks.

Basidiomycetes are fairly common in moss bog, and the fungus *Dictyolus muscigerus* Quél. is found nowhere else. This was found at one spot on the plain of the Russian Base forming "fairy rings" in very wet moss. The mycelia of the various fungi grow amongst the moss. *Peltigera canina* Willd. and an *Evernia* are common, and some other lichens also occur. A few foliose liverworts grow amongst the numerous mosses. Certain species of higher plants were only found in moss bog. These were the following:

Chrysosplenium tetrandrum (Lund) Th. Fries
Cochlearia groenlandica L. var. arctica Schlecht.
Equisetum arvense L.
Eriophorum Scheuchzeri Hoppe
Ranunculus hyperboreus Rottb.
R. lapponicus L.
R. lapponicus L. × Pallasii Schlecht.

The following species are characteristic of, though not confined to, moss bog:

Alopecurus alpinus Sm.
Cardamine pratensis L.
Juncus biglumis L.
Ranunculus sulphureus Soland.
Saxifraga rivularis L.

A number of species occur as frequently elsewhere but often grow in the bogs. The commonest are the following:

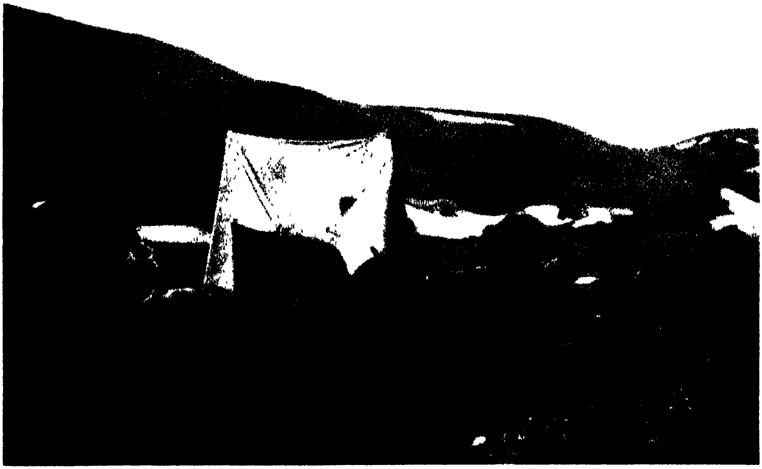
Cardamine bellidifolia L.
Cerastium, hairy forms
C. Regelii Ostenf.
Cochlearia groenlandica L.
Equisetum variegatum Schleich.
Phippsia algida R.Br.
Poa spp.
Salix polaris Wahlenb. } ramifying through
Saxifraga oppositifolia L. } moss hummocks.
S. cernua L.
S. groenlandica L.
S. Hirculus L.
S. nivalis L.
S. comosa Fellm.

Usually ordinary fjaeldmark grades into adjacent moss bog by the gradual disappearance of the drought-loving species, the thinning out of flowering plants and lichens generally, the coming in of *Ranunculus sulphureus* Soland., and the increase in the moss hummocks, which eventually meet to form a closed community.

The next three types may be grouped as **Dry Closed Communities.** On the plain of the Russian Base what may be called **Grass-Moss Closed Community** was found. This community was intermediate between moss bog and fjaeldmark, but differed from the usual, open, tussocky, intermediate vegetation in being closed, not hummocky, and dominated by mosses. The mosses were much less luxuriant than in the bogs and were to some extent replaced by lichens. *Poa* sp. or spp., *Alopecurus alpinus* Sm. and *Salix polaris* Wahlenb. formed abundant patches in parts, while in other places the grasses were thinly but evenly spread through the moss. Other flowering plants were rather scarce and grew on the higher and drier patches. The following is a complete list of the plants found:

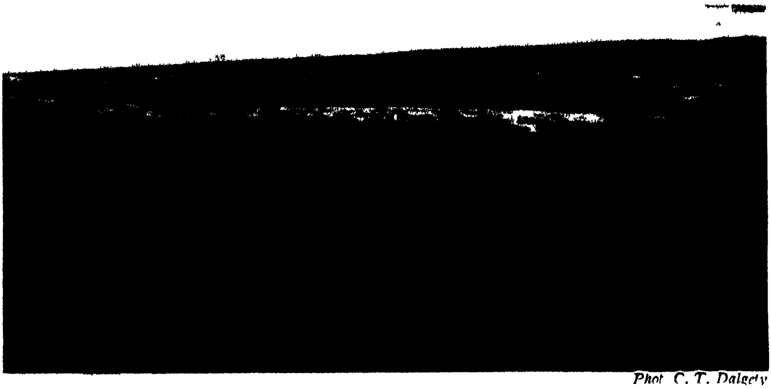
Alopecurus alpinus Sm.
Cardamine bellidifolia L., common
Cerastium, hairy forms
C. Regelii Ostenf.
Cochlearia groenlandica L.
Draba sp., yellow-flowered
Equisetum variegatum Schleich.
Eriophorum Scheuchzeri Hoppe
Luzula confusa Lindeb.
Oxyria digyna Hill
Papaver radicatum Rottb.
Pedicularis hirsuta L.
Poa sp. or spp.
Ranunculus sulphureus Soland.
Salix polaris Wahlenb.
Saxifraga cernua L.
S. groenlandica L.
S. Hirculus L.
S. nivalis L.
S. oppositifolia L.
S. rivularis L.
Stellaria longipes Goldie

This list includes many of the chief fjaeldmark species, and no doubt others could be found, if this local community were developed elsewhere. The presence of *Eriophorum Scheuchzeri* Hoppe, *Ranunculus sulphureus* Soland.



Phot. C. T. Dalgety

Phot. 1. Moss-lichen-willow closed community behind the hut at Keilhau Bay.



Phot. C. T. Dalgety

Phot. 2. Deevie Bay, seen from the foot of the hills looking down the outwash slopes, which are fairly barren owing to earth creep and scouring in the flood ater channels. At the foot of the slope is a transverse drainage channel; yond it is the more richly vegetated coastal plain studded with boggy pools.

MICHELMORE—Edge Island, Spitsbergen

and *Saxifraga rivularis* L. indicates the moistness of the habitat, but the more typical bog plants, *Juncus biglumis* L., and the three creeping species of *Ranunculus*, are absent.

Near the hut at Keilhau Bay **Moss-Lichen-Willow Closed Community** occurs over a few square yards between the little bog and the fjaeldmark (Pl. XV, Phot. 1). It is a closed carpet of moss on dry ground and contains lichens and much *Salix polaris* Wahlenb. It is probably boggy in the early part of the summer.

On the coastal plain north-east of the south-eastern end of Negro Vale there is a fairly large area covered with a black encrusting lichen, in which grow scattered plants of the usual fjaeldmark species.

More **Grassy Closed Communities** are rare. Some of the old huts built by hunters round the coast have sods built up round the outside of the walls to a height of 3 or 4 ft., and these support more luxuriant plants of *Poa*, etc., than the ground round about. This luxuriance is probably partly due to the greater warmth received from the sun by the steep sides. The presence of grasses is probably encouraged by an abundance of decaying roots in the sods, for Summerhayes and Elton (**4**, **5**) have shown that manuring by birds deflects the normal succession from a heath to a grass or herb community.

On the coastal plain below the Kuhr Glacier there are some curious, curved, gravelly ridges bearing at intervals little grassy hummocks. The latter may be the "skua hummocks" described by Summerhayes and Elton, although no birds were seen on them. They are clothed with a mossy turf with *Festuca arenaria* Osb., *Polygonum viviparum* L., *Cerastium Regelii* Ostenf., *Stellaria longipes* Goldie, *Saxifraga oppositifolia* L. and other plants. The *Festuca* is confined to the hummocks, but all the other species also grow, less luxuriantly, in the very sparse fjaeldmark around.

Locally a **Rocky Scarp Community** is developed where there are outcrops of hard rock near the coast, facing a warm quarter and with a good water supply. In the shelter given by boulders, or by the scarp itself, is found the most luxuriant and varied vegetation of Edge Island. Mosses cover the soil with thick cushions, and lichens also grow well. The warmth, shelter from winds, protection from scouring water, early melting of the snow, and stability of the soil give the more delicate upright plants better conditions for growth than anywhere else. On the other hand the more compact and hardy fjaeldmark species, adapted though they are to an exposed habitat, are not excluded. As a result this community has a richer flora than any other, only a few of the special bog plants being absent. *Silene acaulis* L., *Potentilla emarginata* Pursh., *P. pulchella* R.Br., *Taraxacum arcticum* Dahlst. and *Trisetum spicatum* Richter. are characteristic of the rocky scarps, the last four being almost confined to them. *Silene acaulis* L., though confined to the dolerite sills, is found also in the fjaeldmark community with which the drier parts of the surfaces of the sills are clothed. *Ranunculus pygmaeus* Wahlenb., *R. sulphureus* Soland. and

Minuartia biflora Schinz. et Thell. grow particularly well on the scarps, as indeed does almost every flowering plant which lives on Edge Island.

By its closed character with mosses dominant this community shows affinity with the moss bog, and it likewise depends, though to a lesser extent, on a permanent supply of water. On the other hand it grades through a **Boulder Fjaeldmark**, which has fewer and poorer higher plants, plenty of lichens and mosses between the rocks, and some bare patches of soil, into the ordinary fjaeldmark.

Aquatic Communities of higher plants hardly exist on Edge Island, for the only species which can grow completely submerged is *Ranunculus hyperboreus* Rottb. It does not flower when growing under water. Mosses only grow in those ponds which look as if they sometimes dry up, being apparently unable to stand perpetual submergence. Filamentous algae are fairly common both in still and in running water.

III. GEOLOGY AND SOIL.

The geology of Edge Island (**2**) is very simple. The rocks are of Triassic age and are all horizontally bedded except for traces of slight folding near Whales Point and Negro Point. They consist of three series of fissile shales, the upper of which contains many inconstant bands of flaggy sandstone and the lowest of which contains calcareous bands. The lowest series of shales is rich in oil, but this appears not to affect the flora. There are numerous faults, but they are too small to affect the topography.

On the west coast a number of dolerite sills are intruded. One large sill, which extends for miles along the north-west coast of Edge Island, has little effect on the vegetation, as it merely forms a scarp two-thirds of the way up the cliffs. Other sills lie at sea-level in the following areas along the west and south coasts of Barents' Island and Edge Island: Changing Point, Cape Barkham, Cape Lee, the Plain of the Russian Base, Andree Island and Diana Bay. This series forms coastal plains and islands, and is of considerable importance to the vegetation.

Owing to the fissile nature of the sedimentary rocks and the lack of a protective covering of plants, the ground is covered almost everywhere with some depth of shaly soil. The sandstone beds give rise to a great quantity of flat stones, which lie on the surface or in the ground or are arranged in patterns in polygon areas. The only rock outcropping on level ground is the dolerite, which is less fissile than the sandstone. Even the cliffs rising behind the coastal plains are almost entirely covered with talus. Only the sandstone bands and the occasional dolerite sills outcrop on the surface except just below the summits, where the slopes are too steep for the talus to remain.

Barents' Island appears to be exactly like Edge Island in geology, topography and botany.

Phot C T Dalgety

Phot 3 North coast of Edge Island Freeman Strait to show the type of coast typical of Edge and Barents Islands

Phot C T Dalgety

Phot 4 Coastal plain showing slight terracing parallel to the shore The small water channel in the foreground is fringed with hummocky vegetation intermediate between fjaeldmark and moss bog

MICHELMORE—Edge Island, Spitsbergen

IV. THE TOPOGRAPHY AND THE DISTRIBUTION OF THE PLANT COMMUNITIES.

The plateau.

Edge Island is a plateau, which rises from the sea or from a relatively narrow coastal plain to hills of 800 to 1200 ft. high (Pl. XVI, Phot. 3). Much of the plateau is covered by an ice cap formed of great domes, which are often many miles across. The highest part of the ice rises to some 2500 ft. The south-eastern corner of the island is the most heavily glaciated part, and 30 miles of the coast are masked by the ice cliffs of the great King John's Glacier. In Deevie Bay the coastal hills and nunataks further inland are free from ice, but several glaciers break through the hills and almost reach the sea. On the west coast the unglaciated belt is several miles wide, and a considerable area in the north is free from ice.

According to the descriptions and photographs of the exploring parties the inland parts of the plateau bear at best a very sparse fjaeldmark and in many places are quite barren.

The tops of the hills near the sea are barren compared with the coastal plains below. In some places nothing grows but encrusting lichens on the stones, and in others plants of the hardier species form ordinary fjaeldmark, and moss cushions are often present. Soil polygons seem to be much commoner than on the coastal plains. In any slight hollow the soil is wet, and the polygons are of the mossy variety, while elsewhere they are drier. Even wet hollows may be quite devoid of higher plants, and the higher and drier parts are commonly so. The conditions of life are evidently much harder on the plateau than down on the coastal plain. This is shown by the general barrenness and by the small number of species present. It was noticed that in chilly weather it might be snowing and freezing at the tops of the cliffs, while it was raining and not freezing below. The snow must lie longer in the spring and come earlier in the autumn, thus curtailing the all too short summer season. The absence of plants from some patches may be due to the snow being blown off them in winter, and not only to drought in summer. The hills are much exposed to winds, but on one occasion it was found that a strong wind blowing nearly parallel to a coastal line of hills was deflected by the facetted spurs, so as to blow straight up the higher cliff slopes with tremendous force and leave the flat hill top in a calm eddy. Such a vertical wind current must be very useful to the plants in carrying their bulbils and seeds upwards. The amount of moss growing on the hill tops suggest that precipitation may be greater or evaporation less than on the coastal plain.

The cliffs.

The plateau is bounded all round the coast by steep slopes which are of almost exactly the same height for miles. Where the cliffs are washed by the sea, they are too steep to be accessible, being made of friable rock. Talus collects however wherever a sandstone band forms a scarp, so that there is probably some vegetation. In places these cliffs are used for nesting by sea birds, and here there is probably the special vegetation described by Summerhayes and Elton (**4, 5**) and others for bird cliffs. Elsewhere the cliffs slope down to a coastal plain at a gradient of usually not much more than 45°. The large valleys running out from the interior are bounded by similar cliff-like slopes, which are steepest at the top owing to their former erosion by ice. The top 50 ft. or so are often so steep that no soil will lie and no plants will grow on them. Below this the slopes are broken into facetted spurs coated with talus, which is too unstable for anything but a sparse ordinary fjaeldmark to develop. The wet ground is so continually shifted by the expansion and contraction of the freezing and melting water, that it is very unstable even on gentle slopes. Any deeply rooting plant would tend to be pulled down-hill, leaving its roots behind in the more stable deeper soil. The plants are widely scattered and consist of a few of the hardiest species. *Saxifraga cernua* L. is the commonest plant, and *Cerastium alpinum* L., *Papaver radicatum* Rottb., *Saxifraga oppositifolia* L. and other species also occur. *S. oppositifolia* L. is interesting as belonging to that creeping and rooting type of plant which is so characteristic of screes in all climates except the dry tropics, where the high temperatures reached by the surface of the ground make its existence impossible.

At Negro Vale it was found that *Cerastium Regelii* Ostenf. and a hairy *Cerastium* occurred together on the floor of the valley, only *C. Regelii* Ostenf. on the gentle outwash slopes at the sides and on the poorly vegetated summit, and *C. alpinum* L. alone on the steep scree-covered sides of the hills. No explanation can be offered, for both kinds normally occur together on the flatter parts of the coastal plain, and both were present on the tops of the hills south of the Delta Glacier.

The outwash slopes.

At the base of the cliffs the accumulations of scree cause the slope to lessen gradually. The streamlets, which rush down the gullies between the spurs during rain or thaw, spread out in small, stony deltas. The delta at the foot of each gully is absolutely barren owing to its being the bed of a torrent, but (Pl. XV, Phot. 2) the intermediate space at the foot of each spur bears a richer and more mossy ordinary fjaeldmark than the slopes above, being watered in moderation by drainage from above and being more stable. Lower down the lessening slope the little alternating barren flood channels and fjaeldmark areas lose their regularity. In places, as on the north side of Cape Lee, the outwash slope continues right down to the sea and covers the plain with silt.

Where the coastal plain is broader, the drainage is often held up at the foot of the steeper slope by the edge of moss bog or rich, mossy fjaeldmark. The mossy vegetation forms by its upward growth a lower bank to the drainage area, which runs at right angles to the slope and parallel to the side of the hill, and is devoid of life and covered with mud and sluggish water. This line marks the highest place where the ground is level enough, and therefore the soil sufficiently stable, to allow the vegetation to take full advantage of the plentiful supply of drainage water.

The valleys.

Several deep ice-free valleys extend some way inland from the west coast, and a similar one probably runs into the sea on the east coast a little south of Cape Heuglin. They have the steep sides and wide floors typical of valleys which have been filled by glaciers. Negro Vale is an isolated fragment of a valley of this type, but it now goes from sea to sea. It is difficult to see how it could in its present position ever have gathered enough ice to feed a glacier of the size which evidently has existed in it in the past. It is therefore possible that the upper end of it has been faulted down beneath the sea since at least the earlier part of the Ice Age.

The south-eastern end of Negro Vale was the only one of these large valleys which was examined botanically, but the following description will probably apply equally well to others, as far as can be judged from the descriptions of the inland surveying parties. Glacial erosion has given the valley steep sides, which later erosion by frost and water has modified into sloping cliffs like those along the coast. There are, therefore, outwash slopes extending into it from the sides. The myriad streams that run from the hills during the thaw and after rain, which is rare, spread over the broad floor of the valley in ever changing stony channels before they join the deeper beds of the larger streams. A great deal of the valley floor therefore resembles the outwash slopes. Only in patches protected from flooding because they are encircled by deep channels can a richer vegetation develop. The general aspect of the vegetation here is extraordinarily like that of the hill tops. There is some ordinary fjaeldmark, but the greater part is markedly polygonated. The polygons are chiefly of the dry type. Sometimes large polygons contain secondary ones, but the borders of the latter do not usually bear plants. The greater shelter and warmth in the valley allow more species to appear than on the plateau.

The chief geographical discovery of the expedition was the finding of a great, open, branching valley, which extends northwards from the head of Deevie Bay into the heart of the ice cap, and which was named Reindeer Valley. Mr N. L. Falcon, who was a member of the cross-country party which found it, told me that the vegetation in the bottom looked from a distance much richer than that of the other large inland valleys. The rivers left by the retreat of the ice have cut canyons into the ice-eroded valley floor. The presence of these canyons and the absence of the steep sides characteristic of the other large valleys must protect the surface of the ground from those wandering flood waters which make much of the floors of the other valleys so barren. It is also possible that the better climate, which Summerhayes and Elton (5) have pointed out as so important for the flora in the interior of the fjords of North-east Land and West Spitsbergen, exists in Reindeer Valley too. Unfortunately the valley was only discovered in the middle of August, and the southward drift of the ice at the end of the month prevented a projected attack on it from the east coast.

The coastal plain.

The emergence of the land, which is thought to be due to the lightening of the load of ice laid on it during the Ice Age, has resulted in a strip of coastal plain running almost all round the coast (Pl. XVI, Phot. 4). Cliffs rising direct from the sea as at Negro Point and Whales Point are the exception. Where there is a break in the hills, as at the Kuhr Glacier and the head of Deevie Bay, or where there is a dolerite sill near sea level, as at the Plain of the Russian Base, the plain may be several miles wide. In other places, as on the north-east side of Cape Lee, it may be only a few yards across.

The coastal plain bears a richer and more varied vegetation than anything inland with the possible exception of parts of Reindeer Valley. The greater part of it is covered with ordinary fjaeldmark, which varies much in luxuriance according to the amount of water present. If conditions are at all favourable, the vegetation is far richer than it is with a similar water supply further inland. Only here and there are there polygons in the fjaeldmark.

On parts of the coastal plain with only a slight slope, as at the south-east end of Negro Vale and in the centre of Keilhau Bay, the ground may be gently waved parallel to the shore. The waves presumably mark stages in the uplifting of the land from the sea. The crests bear ordinary fjaeldmark, and in the troughs little pools and patches of moss bog are formed. Larger pools and patches of bog are caused by the actual sea beach, which in some places is raised a few feet above the level of the land behind it, so as to hold up the water draining down to the sea. Other patches of moss bog occur where water oozes out of the ground in slow springs. Here and there soil polygons are formed in the bog, giving the wettest type of mossy polygon.

At Keilhau Bay and Changing Point the plain is broken into a series of terraces separated by steep slopes about 25 ft. high (Pl. XVII, Phot. 5). The slopes probably mark the position of former low cliffs. Snow, or even ice, lies long on the slopes, so that they are rather barren. At the base of each slope there is a miniature outwash slope like that described above for the larger cliffs bounding the main plateau. The concentrations of surface water found at the feet of such outwash slopes combined with the reflection of heat rays from the sun by the steep banks above are probably the reasons why the richest fjaeldmark to be found in all the country exists below these slopes. Where there are little streams running over the coastal plain, they may either keep to their

Phot. A. P. G. Michelmore

Phot. 5. Changing Point, showing a pond fringed with moss bog and fed by icy snow against a terrace. Being permanent, this pond has no moss on its bottom.

Phot. A. P. G. Michelmore

Phot. 6. Coastal plain below the Kuhr Glacier, made barren by silting from the stream seen in the background.

MICHELMORE—Edge Island, Spitsbergen

beds or spread out into stony deltaic tracts. In the latter case the floods prevent any permanent colonisation by plants. When the streams are more restrained, *Ranunculus pygmaeus* Wahlenb. and *R. sulphureus* Soland. in smaller numbers are often common on the banks.

The dolerite sills.

The sills of the west and south coasts hold water better than the shales, and therefore bear far more extensive and luxuriant moss bogs than any other parts of the coastal plains. The bogs are dotted with shallow ponds of various sizes, and occasionally there are patches of mossy polygon in the drier parts. *Chrysosplenium tetrandrum* (Lund) Th. Fries, *Cochlearia arctica* Schlecht., *Eriophorum Scheuchzeri* Hoppe, *Ranunculus lapponicus* L. and *R. lapponicus* L. × *Pallasii* Schlecht. were only found in bogs on dolerite sills, but this is probably only because moss bog is so poorly developed elsewhere. The drier parts of the surfaces of the sills are in some parts covered with rounded boulders and a vegetation of boulder fjaeldmark. Elsewhere there are bare platforms of rock with ordinary fjaeldmark in the hollows.

The rocky scarp community is confined to the edges of sills with a continuous supply of water from bogs or streams on the upper surface. The sills themselves are limited in extent, and only parts of their edges are well watered. The rocky scarp community is therefore very local.

The only place where the grass-moss closed community was found was on a fairly dry part of the dolerite plain at the Plain of the Russian Base.

The silted areas.

The rivers draining the glaciers which do not quite reach the sea contain a great deal of fine mud. Where they debouch on to the coastal plain they may spread out and form large mud flats with sluggish channels winding about in them. These areas (Pl. XVII, Phot. 6) are quite barren except at their edges, where a wretched fjaeldmark community manages to exist. In times of flood they are subject to strong currents, which would root out plants in some places and cover them with mud in others. The fine sand and mud covering the outer parts of the silted areas dry quickly, and plants which have withstood the floods of the spring thaw then have to suffer all the trials of existence in a desert.

Somewhat similar conditions can exist apart from glaciers, as at Cape Lee, where there is a long shore-line kept rather barren by the outwash from the high cliffs behind. The outwash here reaches the sea, depositing the stones in the usual tract at the foot of the cliffs, and spreading fine sand and mud all over the sloping plain, instead of collecting into definite stream beds in the normal way.

The moraines.

Three large moraines were examined in all, those of the Kuhr Glacier on Edge Island, the Freeman Strait Glacier on Barents' Island and the Hayes Glacier in Mohn Bay on West Spitsbergen.

The surface of the moraines is thrown into a jumble of steep hillocks without any definite arrangement. Between the hillocks are hollows, some of which lead into little valleys draining the moraine, while others have no opening and contain small temporary or permanent pools. In the Kuhr Glacier the part of the moraine facing the tip of the glacier is flowing in a terrible quagmire of liquid mud back into a large lagoon lying between the glacier and the moraine. This is naturally devoid of plants.

The vegetation of the moraines is puzzling, for it is sparse without any apparent reason. The soil, though stony, is less so than that produced by the weathering of the shaly country rock *in situ*. The matrix is on the whole finer, but it contains particles of all sizes. The tilth looks much better, and the moraine soil seems to hold moisture better, yet the moraines seem unable to support as rich a vegetation as any well-watered area of shaly soil.

On the moraine of the Kuhr Glacier the vegetation can be divided into two facies, a wet and a dry. The wet facies occurs in the beds of the temporary pools and at the edges of some permanent ponds. It consists almost entirely of *Polygonum viviparum* L. and *Salix polaris* Wahlenb. growing amongst not very luxuriant mosses, and is a form of the moss bog community. The dry facies is a fjaeldmark, in which the following species were found:

Alopecurus alpinus Sm.
Braya purpurascens Bunge
*Cerastium, hairy forms
*C. Regelii Ostenf.
Cochlearia groenlandica L.
Draba 2 (?) spp. of alpina group
Festuca arenaria Osb.
F. brevifolia R.Br. (?)
Juncus biglumis L.
*Oxyria digyna Hill
*Papaver radicatum Rottb.
Phippsia algida R.Br.
Poa, mostly viviparous forms, probably hybrids of P. alpigena Lindm.
*Polygonum viviparum L.
Potentilla pulchella R.Br. (1 plant)
Salix polaris Wahlenb.
Saxifraga cernua L.
S. groenlandica L.
*S. oppositifolia L.
Stellaria longipes Goldie
Taraxacum arcticum Dahlst. (1 plant)

The common species are marked with asterisks. The chief points to notice are the extraordinary abundance of *Polygonum viviparum* L. and *Oxyria digyna* Hill, and the presence of *Braya purpurascens* Bunge and of the grass believed to be *Festuca brevifolia* R.Br. Even the dry facies is confined to patches, and large areas are quite barren.

The moraine of the Hayes Glacier is peculiar in bearing no plant at all except this same grass, probably *F. brevifolia* R.Br., which is quite common. No permanent ponds were seen, and the temporary ones were quite barren. The Freeman Strait Glacier moraine agrees with that of the Kuhr Glacier in general and also produces *Braya purpurascens* Bunge. The only other places where this plant was found were the moraine of the Kuhr Glacier and the silted plain below it. As the silt is all derived from the glacier, it appears that there is some connection between this species and glacier soil.

V. THE WEST COAST OF STOR FJORD.

At Whales Bay we landed by an old hut on the north shore, where there is a platform of hard sandstone raised some feet above sea level. On the inland side of the outcrop is a moss bog with several shallow ponds. Here there is a much greater abundance, luxuriance and variety of grasses than anywhere on Edge Island. The drier parts of the platform are too bare of soil to support much besides encrusting lichens and tufts of *Luzula confusa* Lindeb. and *Salix polaris* Wahlenb. In damp and sheltered crevices a rocky scarp community occurs. In this the component plants grow luxuriantly, *Saxifraga cernua* L. and *Melandryum apetalum* Fenzl. for instance, growing taller, and *Potentilla emarginata* Pursh. and *Taraxacum arcticum* Dahlst. being more abundant and forming larger cushions than anywhere on Edge Island. On the gentle slopes inland a rich ordinary fjaeldmark community occurs. Both here and on the sandstone outcrop *Dryas octopetala* L. and *Salix polaris* Wahlenb. × *herbacea* L. are common and luxuriant. The hill on the west side of the hut was climbed, and the walk revealed the surprising fact that the rich fjaeldmark of the plain dwindled away to nothing at a few hundred feet above sea-level. On the summit there was practically nothing except a few isolated plants of *Papaver radicatum* Rottb. and *Saxifraga cernua* L. The barrenness of the top is probably due to the pointed nature of the hills, which become very dry on top, unlike the Edge Island hills, whose flat tops hold a lot of water.

The next place visited after Whales Bay was the north-east side of Agardh Bay. Here there is a coastal terrace sloping gently from the hills for about 2 miles, down to a low sea cliff about 12 ft. high. The cliff section shows horizontal beds of fissile sandstone with a little raised beach deposit on top. This was one of the most barren spots seen by me during the whole expedition. On the outer parts of the coastal plain nothing grows save a few wretched mosses (*Polytrichum*) and the usual encrusting lichens. Further inland by a stream there is a little more vegetation, the following plants being found:

Alopecurus alpinus Sm.
Cerastium, hairy form
Deschampsia alpina R. et Sch.
Luzula confusa Lindeb.
Papaver radicatum Rottb.
Phippsia algida R.Br.
Poa rigens Hartm.
Poa, viviparous form, probably hybrid of P. alpigena Lindm.
Polytrichum (sp.)
Ranunculus sulphureus Soland.
Saxifraga nivalis L. or tenuis H.Sm.
Stellaria longipes Goldie

The hills were not actually reached, but from a little distance they looked as barren as the plain.

At Mohn Bay the shore, the moraine and the dolerite sill were visited. The shore is barren and the moraine has already been dealt with above. On the scarp of the sill facing the glacier there is a fine display of poppies (*Papaver* *radicatum* Rottb.). The drier parts of the top of the sill bear little but abundant mats of *Dryas octopetala* L. and *Salix polaris* Wahlenb. with some *Saxifraga cernua* L. and *S. oppositifolia* L. On the moister parts and round some temporary standing water there is a moderately rich fjaeldmark, in which the following plants were found:

Alopecurus alpinus Sm.
Cardamine pratensis L.
Cerastium Regelii Ostenf.
Deschampsia alpina R. et Sch.
Draba sp. of alpina group
Dryas octopetala L.
Equisetum arvense L.
Festuca arenaria Osb.
Juncus biglumis L.
Melandryum apetalum Fenzl. (1 plant)
Oxyria digyna Hill
Papaver radicatum Rottb.
Poa, viviparous form, probably hybrid of P. alpigena Lindm.
Polygonum viviparum L.
Ranunculus sulphureus Soland.
Sagina intermedia Fenzl.
Salix polaris Wahlenb.
S. polaris Wahlenb. × herbacea L.
Saxifraga cernua L.
S. groenlandica L.
S. nivalis L. or tenuis H.Sm.
S. oppositifolia L.
Stellaria longipes Goldie
Two unidentified grasses

A special development of rocky scarp community is not found here, the requisite conditions being absent. The slope of the mountain behind looks barren when viewed from the sill.

VI. SUMMERHAYES AND ELTON'S CLIMATIC ZONES.

All the places visited on the east of Stor Fjord unquestionably belong to one zone. This is most clearly shown by the close resemblance between Changing Point, in the north-west of Barents' Island, and Keilhau Bay, in the south-west of Edge Island, in flora and vegetation as well as in physiography. The other places vary, but in all cases the differences agree with what would be expected from observed conditions of three main factors, height above sea level, water supply and nature of substratum (whether hard rock or shaly soil, whether level and stable or sloping and subject to earth creep, and whether liable to scouring or silting over by streams).

On the other hand Whales, Agardh and Mohn Bays do not fit into the same group at all. The general surface of the country seems to be much more barren than on the other side of Stor Fjord, and yet a favourable spot like the neighbourhood of the hut at Whales Bay produces a finer vegetation than exists anywhere on the opposite shores. The flora appears to be richer, as is shown by the more important part played by grasses and the greater abundance or luxuriance of other plants which are absent or local on Edge Island, such as *Salix polaris* Wahlenb. × *herbacea* L. (absent on east side of Stor Fjord), *Dryas octopetala* (Cape Lee only), *Melandryum apetalum* Fenzl., *Potentilla emarginata* Pursh. and *Taraxacum arcticum* Dahlst. Admittedly a number of plants were found in Edge Island and not on the west side of Stor Fjord, but the time spent in the latter was too short to enable any arguments to be based on this.

Summerhayes and Elton's observations (5) on the effects of fog on the vegetation of Spitsbergen suggest that these differences in vegetation may be due to differences in climate existing between the opposite sides of Stor Fjord.

We know from experience that the east side is very foggy. If the west side were less so, it would explain the distribution of the plants. It does not rain much in Spitsbergen, so that much of the moisture of the surface of the ground must be due to, or at least be conserved by, the fogs. Absence of fog would make much drier those parts of the country which were not watered from the glaciers, and would thus produce that general barrenness so conspicuous on the west side of Stor Fjord. On the other hand the presence of drainage water near streams and ponds would remove this limiting factor of drought in certain places and enable the plants to take full advantage of the greater amount of sunshine. There would then exist the state of things which we see, the general surface of the country more barren, but the neighbourhood of drainage water bearing a richer vegetation and a larger flora, than in the more foggy zone.

Summerhayes and Elton divided the vegetation of Spitsbergen into zones—(1) the Barren zone, (2) the *Dryas* zone, (3) the *Cassiope* zone, and (4) the inner Fjord zone. They provisionally included Stor Fjord in their *Dryas* zone. The coast of Edge Island east of Mt. Middendorf on the north and Diana Bay in the south, the eastern half of Barents' Island and the south of West Spitsbergen from a little south of Whales Bay, were put in the Barren zone. On the whole I agree with this arrangement, though I should be inclined to push the boundaries of the Barren zone a little further east on Barents' Island and Edge Island. On West Spitsbergen this boundary should probably be put a good deal nearer South Cape, for the richest vegetation seen anywhere by me was at Whales Bay, and this is quite near the edge of the Barren zone as shown on Summerhayes and Elton's map.

In south-east Spitsbergen their *Dryas* zone can be divided into two sub-zones, the *Dryas* sub-zone proper, as described above for the west side of Stor Fjord and characterised by *Dryas*, and the Edge Island—Barents' Island type without *Dryas* and with the other characteristics described in Section II of this paper. In the present state of knowledge it is better not to try and apply this throughout Spitsbergen, as the zones elsewhere grade into one another, and the subdivisions may differ on different geological formations.

In discussing Stor Fjord Summerhayes and Elton suggest that the occurrence of *Eriophorum Scheuchzeri* Hoppe and other plants may indicate an even better climate than that of the *Dryas* zone and state that this cotton-grass is characteristic of the *Cassiope* zone. *Eriophorum Scheuchzeri* was found at each of the three places in Stor Fjord where moss bog was best developed, the Plain of the Russian Base, Andrée Island and Whales Bay. It therefore seems to be a regular inhabitant of the *Dryas* zone in south-east Spitsbergen and even of the more barren Edge Island and Barents' Island sub-zone. Probably this and the other uncommon bog plants found on Edge Island are hardy enough with regard to the weather but are less virile than the commoner species in other ways. Some of the fjaeldmark plants occur only here and there, and it is natural that the less successful bog plants also should not grow in every bog. As large bogs are confined to the occasional outcrops of dolerite or sandstone in south-east Spitsbergen, some bog species, even if hardy, are bound to be rare.

VII. PLANTS AND SOIL.

In Sections II, IV and V the important part played by water supply in the arrangement of the vegetation has been stressed. The uniformity of geology and topography of Edge Island and Barents' Island simplifies the matter and makes it easy to work out the action of the water supply, but it also makes the area an unsuitable one for a study of the effect of soil. However, a few indications that the soil does have some direct effect on the type of vegetation have already been mentioned, and they will be discussed here in the light of Summerhayes and Elton's work.

The sandstone platform of Whales Bay appears to react on the vegetation exactly like the dolerite sills. Both owe their essential characteristics to their being horizontal outcrops of hard rock, which hold up drainage water on their surfaces. There is no indication of any chemical difference between their effects on the vegetation.

The grass-moss closed community described on p. 162 was only found on dolerite. On p. 163 another closed community rich in lichens is mentioned as occurring near the mouth of Negro Vale. This area is said by Falcon (**2**) to be also of dolerite. Unfortunately neither my notes nor my memory give any clue as to whether this community was actually on the dolerite. Although it is interesting to note that no appreciable area of such communities occurred anywhere else, these two cases alone would not be enough to generalise on, for the communities covered only a small fraction of the total area of dolerite examined in the course of the expedition. However, Summerhayes and Elton (**5**) state that there is a greater tendency for "heaths" to develop on dolerite and on granite and gneiss than on sandstone or shale. A close study of the mosses and lichens would be necessary to enable one to find out the reason for this.

The marked effect of manuring on the vegetation of the Arctic has often been noticed, and two probable instances of this are described under "grassy closed communities" on p. 163. Manuring does not necessarily produce a closed turf at once. Round the old hut on the coast numbers of bones testify to the amount of animal matter which the hunters must have scattered near their temporary homes. The effect on the vegetation is chiefly the abundance and luxuriant growth of *Cochlearia groenlandica* L., *Phippsia algida* R.Br., *Saxifraga cernua* L. and *S. rivularis* L. The only bird cliff examined for plants was one in Freeman Strait, on which there was a colony of Kittiwakes. Underneath this there was a great deal of *Cochlearia groenlandica* L., which is perhaps the most susceptible of all Spitsbergen plants to manuring. Bird islands exist in several places round the coast, but none was explored botanically.

Summerhayes and Elton (**5**, p. 219) describe a coastal belt in Reindeer Peninsula, in which the vegetation is apparently affected by salt spray from the sea. Nothing of this sort was noticed during the Edge Island Expedition, though it might have been found if its existence had been known of at the time. No salt marshes, such as these authors and Walton (**6**) have described, were found, the only possible localities, the neighbourhoods of the Kuhr and Delta Glaciers, being barren.

Certain peculiarities of the moraines, such as the attachment of *Braya purpurascens* Bunge and of the grass suspected of being *Festuca brevifolia* R.Br. to moraine soil, have already been commented on. It is not possible to say whether the governing factor is physical or chemical, but the occurrence of *Braya purpurascens* on moraine silt which has been redeposited by water, so that its texture is quite changed, is suggestive.

Silene acaulis L. grows both in the rocky scarp community and in fjaeldmark on dolerite, but does not occur on other geological formations in this area. This may indicate adaptation to rocky ground, for it has a long, tough tap root, which may not be well fitted for the probably badly aerated clay soil formed on shales. It might be supposed that some of the other characteristic plants of the rocky scarp community, the *Taraxacum* and the two species of *Potentilla*, were also special hard rock species, but their occasional occurrence elsewhere suggests that they are not so. Probably they are species which have only got a weak footing in this area, and which can only exist in unusually favourable conditions. It so happens that in this area such conditions only occur at the edges of hard rock outcrops, to which these species are therefore almost confined. The same thing is true of *Dryas octopetala* L. on the west side of Stor Fjord.

VIII. SUMMARY.

1. *Plant communities.* The vegetation of Edge Island and Barents' Island consists almost entirely of two types of community, open fjaeldmark and closed moss bog, of which the former covers by far the greater area. A more luxuriant community occurs in a few places on rocky scarp; this is believed to be not directly dependent on a rocky substratum, but to be merely the expression of the most favourable conditions for water supply, aeration of soil and warmth, which on these islands happen to be found only on the dolerite sills. Other closed communities exist very locally. The appearance and floristic composition of all these communities is described.

2. *Succession.* True vegetational succession, *i.e.* the development of the vegetation of an area through different stages, apart from changes induced through the action on the soil of external factors, such as denudation and continued manuring by birds, is believed to be rare, and to be confined to

such small scale processes as the development in fjaeldmark of moss hummocks with their dependent flora. This is because the severity of the climate prevents the potential succession of the vegetation from rising above the initial pioneer stages.

3. *Environmental factors.* A description of the influence of the topography on the vegetation is given. This brings out the fact that the most important factor causing variation in the vegetation within this area is water supply to the roots. It is the amount of water available which decides whether the vegetation in any spot shall be fjaeldmark, moss bog or an intermediate form of community. Drainage water also commonly has a detrimental effect through scouring the surface of the ground and less often by silting. Instability of soil through earth creep on slopes has a restraining influence on the vegetation. The second most important factor is variation in the severity of the climate. This is most clearly shown in the difference in the vegetation near the shore and on the hill tops or in the inland valleys. To a lesser degree it is shown in the effect of shelter or a sunny aspect on slopes. There is some evidence that soil factors other than the availability of water to some extent modify the vegetation and especially the floral composition. The effects are described, but the causes are not understood, except in the case of organic manuring by bird dung or human refuse.

4. *Climatic zonation.* Confirmation is given to the view of Summerhayes and Elton that the coasts of Stor Fjord belong to their *Dryas* zone. The vegetation of three places on the west side of Stor Fjord is described. It differs from that of Edge Island and Barents' Island in being generally more barren but in certain spots more luxuriant and with floristic differences. It is suggested that this is due to there being less fog, a theory which needs to be proved by actual observation of the climate. The more favourable zones in Spitsbergen are on the whole more xerophytic than the more barren zones.

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ECOLOGY OF CERTAIN PLANT COMMUNITIES OF THE CENTRAL PROVINCE, TANGANYIKA TERRITORY[1]

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(*With Plates XVIII–XXII and nine Figures in the Text.*)

CONTENTS.

PAGE
INTRODUCTION 177
SITUATION AND SOILS OF THE KIKORI AREA 178
CLIMATIC CONDITIONS 178
OBJECTS AND METHODS OF THE INVESTIGATION 187
  Aerial factors 188
  Succession 189
  Rates of growth 189
  Soils 190
SYNECOLOGICAL TERMS USED 194
THE CHIEF COMMUNITIES 194
  A. "Mbuga" stream-bed community 194
  B. Seasonal swamp ("Mbuga") community 197
  C. Ecotone of "Mbuga"-*Acacia* spp. 199
  D. Consocies of *Acacia formicarum* 201
  E. Consocies of *Acacia usambarensis* 204
  F. Ecotone of *Acacia usambarensis-Berlinia-Combretum*-Other species 206
  G. *Combretum*-Other spp. Open Woodland 208
  H. *Berlinia* woodland 211
  K. Upland consocies of *Brachystegia microphylla* . . 213
EFFECTS OF PROTECTION FROM FIRE 214
GROWTH INCREMENTS IN HEIGHT AND GIRTH 221
PHENOLOGY 225
CONCLUSIONS 225
SUMMARY 228
ACKNOWLEDGMENTS 229
REFERENCES 229

INTRODUCTION.

THE following is a preliminary account of the results obtained from the study of a number of the main vegetation communities in the Eastern "Fly Belt" of the Central Province, Tanganyika Territory. This study was carried out at the same time as the study of the behaviour and reactions of the Tsetse Fly (*Glossina morsitans* Westw.) in these vegetation communities.

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[1] Cornwall and York Prize for the best M.Sc. thesis, 1933.

It has long been realised that certain species of fly are found, as a rule, only in certain types of vegetation and that, in these types, a particular species of fly prefers some to others. Different writers have stressed this point but it was only in 1929 that a scheme of research (outlined by Dr John Phillips of the Department of Tsetse Research, Tanganyika Territory), by which the factors or factor complexes within these vegetation communities might be studied, was embarked upon. Dr Phillips pointed out that it was not the vegetation community as such, but the habitat conditions within that community, which had a definite attraction or otherwise for the fly. These habitat conditions cannot be elucidated without a study of the vegetation itself. It was extremely unfortunate that this study had to be discontinued before it had advanced beyond the preliminary stages, but the results obtained are worth placing on record.

SITUATION AND SOILS OF THE KIKORI AREA.

The southern part of the Great Masai Steppe is bounded on the western side by an escarpment, rising some 1000–1500 ft. above the plain. On the lower slopes and at the foot of the escarpment, running out for about 6 miles, is a strip of vegetation composed of nine or ten main plant communities and comprising what is known as the Eastern Fly Belt of the Central Province. Towards the northern end of this belt, at an altitude of 4158 ft. and about 45 miles north of Kondoa Irangi, lies the native village of Kikori whose approximate bearings are lat. 4° 25′ S., long. 35° 19′ E. The ecological station of the Department of Tsetse Research was laid out near Kikori village early in 1929, and intensive study of the vegetation and of the Tsetse fly within that vegetation was begun in July 1929.

Using Vageler's classification of the soils of Ugogo (as employed by Phillips (1930)), the principal soil types at Kikori may be classified into the grey eluvial and alluvial soils.

The eluvial soils upon the hill slopes are shallow, overlying gneiss and granite to a depth ranging from several feet to a few inches only. At the foot of the escarpment, however, they are much deeper. These eluvial soils range from sand to sandy loams and are well drained. They gradually merge into the alluvial soils of the "steppe" or plateau below, which are very deep and range from light loams to the heavy clays of the poorly drained "mbugas" or seasonal swamps.

CLIMATIC CONDITIONS.

Up to the present there have been few data on which to base statements regarding the climate of this portion of the Central Province. Nash (1930) has published temperature and rainfall figures for the Entomological Station, Kikori, from one year's data. He divides the seasons into four—two dry and two wet, viz. the long dry season, the light rains, the short dry season, and the heavy rains. He points out that, although the short dry season is really a dry period, the fact is masked by rainfall figures which are comparatively high owing to occasional storms. He shows it to be a period of high temperatures and low humidities.

The writer, while agreeing with this classification of the seasons, would point out that, in some years —e.g. 1930 —the break between the first and second rainy seasons is very short indeed and there is no sudden rise in temperature or drop in humidity (see Tables III, IV, and Figs. 2, 3). The terms first and second rainy seasons instead of light and heavy rains are used advisedly for, in some years, the rainfall for the first season may total as much as that for the second season and the proportion of amount of rain to the number of rainy days in the former may be as great as, if not greater than, in the latter.

SUNSHINE AND LIGHT INTENSITY.

(Tables I, II, and Fig. 1.)

In normal seasons there are two sunshine maxima: (1) at the end of the long dry season or beginning of the first rainy season, and (2) during the short dry season. The absolute minimum is reached during the second rainy season, usually in April. The actual amount of sunshine recorded by a Campbell-Stokes sunshine recorder at any time of the year is only about two-fifths to one half of the possible amount, calculated from the Nautical Almanac (see Table I).

Table I. *Possible and actual hours of sunshine,* 1930.

Date	Possible hours Hr. min.	Actual mean hours per day for whole month Hr. min.	Ratio of possible to actual sunshine
March 21st, 1930	12 6	4 6	2·6 : 1
June 21st, 1930	11 52	4 8	2·5 : 1
Sept. 21st, 1930	12 6	5 5	2·2 : 1
Dec. 21st, 1930	12 25	6 7	1·9 : 1

Heikde (1923) suggests that the mean cloudiness for this region ranges from four- to five-tenths of the expanse of the sky, but the writer is inclined to put it at a higher figure. Data collected for the hours of 8.30 a.m., 12 noon, and 4.30 p.m. daily (Table II) show a range of mean cloudiness per month at 8.30 a.m. of 6·6–9·7, at noon of 3·6–8·5, and at 4.30 p.m. of 3·3–7·3 in tenths of the sky, giving a general mean of seven-tenths. If the mean cloudiness, for each month, be plotted on the same diagram as the mean sunshine per day for each month (Fig. 1), it will be seen that there is a fairly close agreement between the two curves; i.e. as mean cloudiness increases, mean sunshine per day decreases and *vice versa.*

From Table II it can be seen that the mornings throughout the year are cloudy, that at midday the clouds are much fewer and in the afternoon, with the exception of the end of the long dry season (October and November) when thunderstorms occur in the late afternoon, there are fewer still. It is also very striking that after the second rainy season (during July and August), there are mists or low-lying clouds which do not clear till well after midday. The

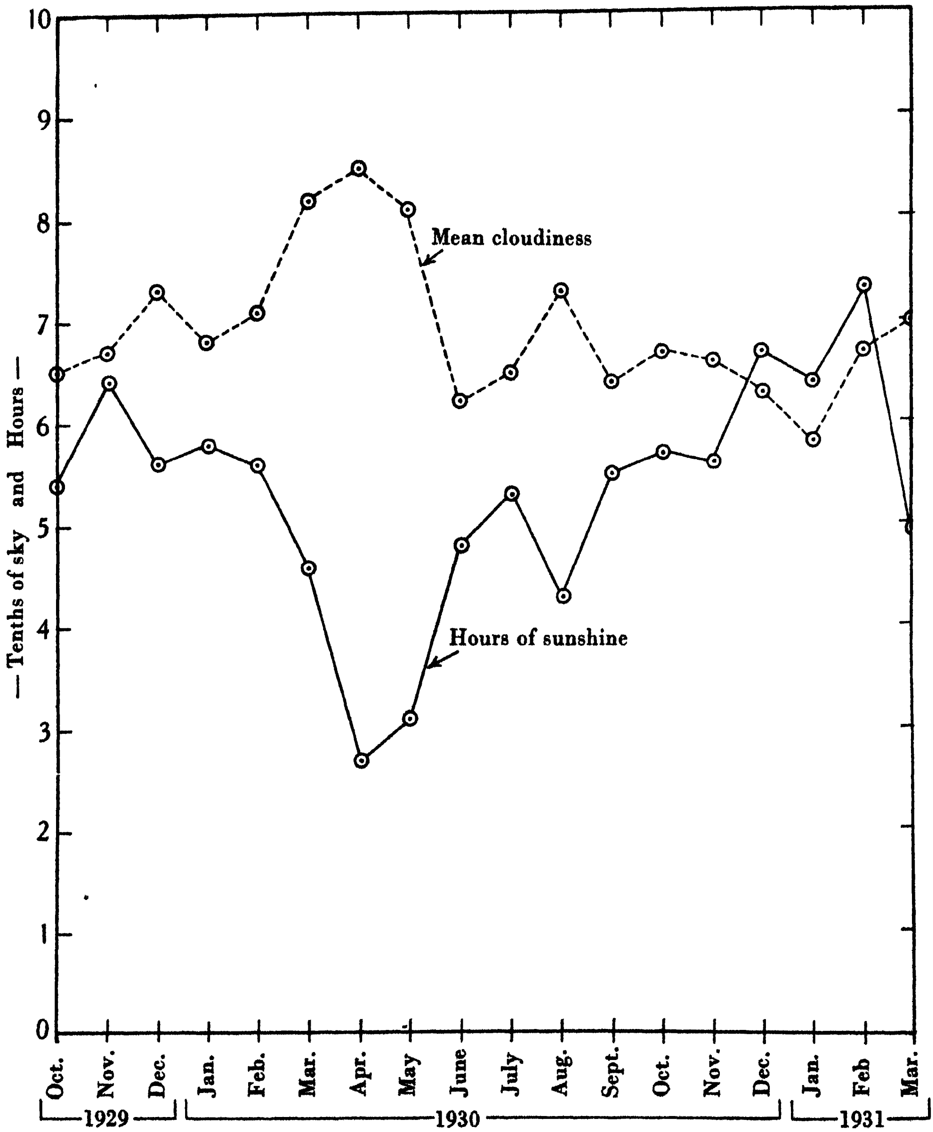

FIG. 1. Mean cloudiness in tenths of sky and hours of sunshine for 1930 and part of 1929 and 1931.

tables show that the noon readings of mean cloudiness for this period of the year are the highest of all the noon readings, while the afternoon readings are the lowest.

Table II. *Mean cloudiness in tenths of the expanse of the sky.*

	Mean cloudiness			Mean cloudiness per day in tenths	Mean sunshine per day in hours
	At 8.30 a.m.	At noon	At 4.30 p.m.		
1929					
Oct.	7·5	4·3	5·8	6·5	5·4
Nov.	8·2	3·6	5·4	6·7	6·4
Dec.	7·6	7·7	6·7	7·3	5·6
1930					
Jan.	7·2	6·3	6·4	6·8	5·8
Feb.	8·6	3·8	6·0	7·1	5·6
Mar.	9·3	5·3	7·1	8·2	4·6
Apr.	9·7	6·3	7·3	8·5	2·7
May	9·1	6·4	7·1	8·1	3·1
June	8·6	6·0	3·3	6·2	4·8
July	8·2	8·2	3·8	6·5	5·3
Aug.	9·4	8·5	3·6	7·3	4·3
Sept.	8·2	—	4·0	6·4	5·5
Oct.	8·5	5·6	5·1	6·7	5·7
Nov.	7·5	5·7	6·0	6·6	5·6
Dec.	6·7	5·2	5·2	6·3	6·7
1931					
Jan.	6·6	4·8	5·5	5·8	6·4
Feb.	7·1	—	6·1	6·7	7·3
Mar.	7·8	—	6·0	7·0	4·9

Quantitative light measurements were taken by means of the improved Eder-Hecht "Dauer-Graukeilphotometer." Phillips, Scott and Moggridge (1931) have published the data obtained. In their paper it is shown that values, even for diffused light (the ratio of diffused to direct light, as measured by the Clements' stopwatch photometer, being as 1 : 3) are very high indeed; much higher, in fact, than any values obtained for stations in other parts of the world by Dorno (1927, p. 370). As might be expected there is a distinct correlation between the Bunsen-Roscoe values, obtained from the Eder-Hecht photometer, and hours of direct sunshine, registered by means of the Campbell-Stokes sunshine recorder.

Maximum light values occur towards the end of the long dry season and during the short dry season, while minimum values are obtained towards the end of the second rainy season.

TEMPERATURE.

(Table III, and Fig. 2.)

As stated by Phillips (1930), the annual temperature phases depend upon the angle of the sun and the incidence of the dry and rainy seasons. The minimum temperatures occur in July or August, at the beginning of the long dry season, just after the sun has reached its minimum angle. This is followed by an increase in temperature until the end of the long dry season (November), shortly after the sun has reached its zenith. The temperatures decrease slightly in December and January, but a second maximum may occur in February. In some years (e.g. 1930) after much rain has fallen in the first rainy season, there may be no rise in temperature in February. The temperatures decrease until the minimum is again reached in July or August (see Fig. 2).

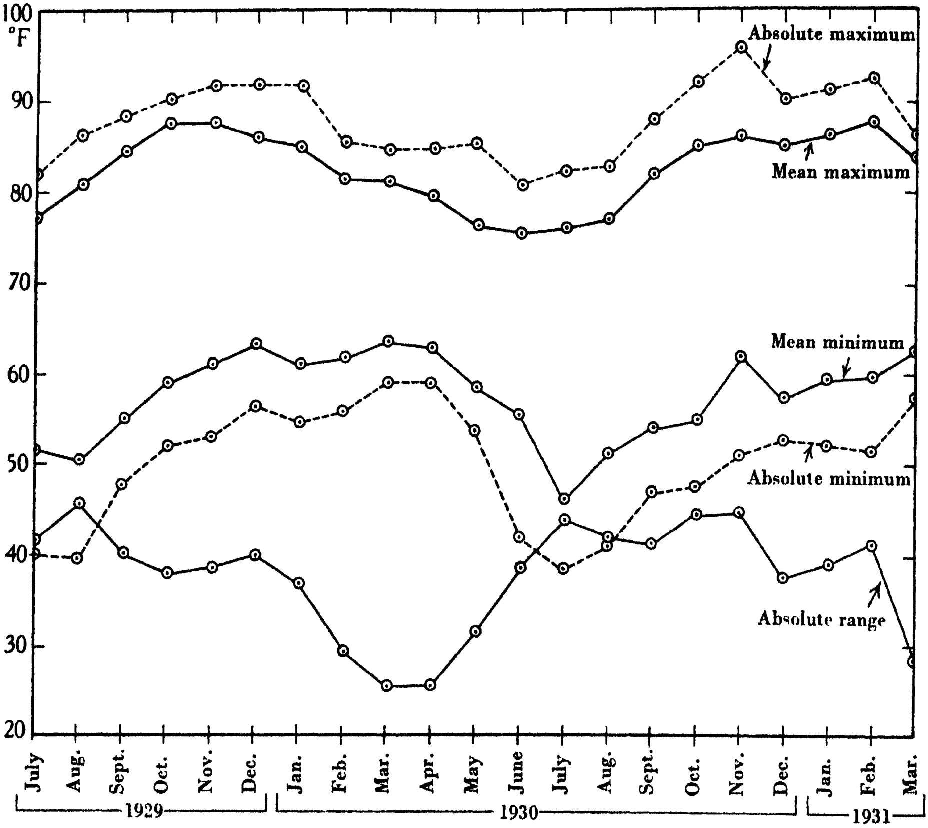

Fig. 2. Absolute and mean maxima and minima and absolute ranges of temperature.

Table III. *Temperatures (Fahrenheit) from thermometers in Stevenson's screens in standard station.*

	Abs. max.		Mean max.		Abs. min.		Mean min.		Abs. range	
	1929–30	1930–1	1929–30	1930–1	1929–30	1930–1	1929–30	1930–1	1929–30	1930–1
July	81·75	82·50	77·25	76·10	40·00	38·50	51·50	46·23	41·75	44·00
Aug.	86·25	83·00	80·76	76·98	39·50	41·00	50·45	51·32	46·75	42·00
Sept.	88·25	88·00	84·58	81·98	48·00	46·75	55·07	53·88	40·25	41·25
Oct.	90·25	92·00	87·46	85·07	52·00	47·50	59·05	54·80	38·25	44·50
Nov.	91·75	95·75	87·45	86·14	53·00	51·00	60·99	61·71	38·75	44·75
Dec.	91·75	90·00	85·87	85·09	56·50	52·50	63·29	57·24	40·25	37·50
Jan.	91·75	91·00	85·09	86·09	54·75	52·00	61·15	59·30	37·00	39·00
Feb.	85·50	92·25	81·44	87·37	56·00	51·25	61·71	59·52	29·50	41·00
Mar.	84·75	85·50	81·32	83·46	59·00	57·25	63·62	62·23	25·75	28·25
Apr.	84·75	—	79·81	—	59·00	—	62·77	—	25·75	—
May	85·50	—	76·25	—	53·75	—	58·56	—	31·75	—
June	80·75	—	75·57	—	42·00	—	50·61	—	38·75	—

The greatest range in difference between maximum and minimum temperatures occurs during the long dry season while, in March and April, during the second rainy season, the range is comparatively small (see Table III).

HUMIDITY AND EVAPORATION.

(Tables IV, V, and Figs. 3, 4.)

Humidity data, worked in terms of Saturation Deficit which (as compared with relative humidity) is an absolute value[1], for the hours of 8.30 a.m., 2 p.m. and 6 p.m. for 2 days (Tuesday and Friday) each week (calculated from a recording hygrometer) show a maximum humidity during the second rainy season (see Table IV and Fig. 3). After that the humidity decreases until the end of the long dry season in October or November. This is followed by an increase till the middle of the second wet season. There may be a decrease in humidity in February during the short dry season, depending on its duration and the rainfall of the previous season. Nash (1930) records as low a relative humidity as 12 per cent. at a temperature of 105° F. in February, 1929.

Table IV. *Mean saturation deficit expressed in millibars.*

	8.30 a.m.		2 p.m.		6 p.m.	
	1929-30	1930-1	1929-30	1930-1	1929-30	1930-1
July	1·9	2·1	17·5	13·7	17·0	2·5
Aug.	4·3	1·8	21·4	15·5	16·4	7·9
Sept.	5·3	2·1	28·1	17·5	22·7	12·9
Oct.	6·5	3·2	24·6	22·3	26·6	15·2
Nov.	5·6	3·0	30·2	21·6	21·8	12·8
Dec.	5·0	4·3	19·7	21·1	12·5	12·5
Jan.	5·8	3·3	15·2	20·0	12·5	7·6
Feb.	3·2	1·9	14·9	17·0	3·4	9·2
Mar.	3·4	2·3	9·6	13·6	1·7	3·0
Apr.	2·3	—	11·4	—	1·7	—
May	1·8	—	10·0	—	1·5	—
June	2·1	—	12·5	—	1·9	—

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[1] *Saturation deficit* (see Phillips, 1931, "Forest Succession and Ecology in the Knysna Region," *Botanical Survey of South Africa*, Memoir 14, p. 74) is the *lack* of vapour pressure, that is, the difference between the actual vapour pressure and the amount which the air would contain at the current temperature, were the atmosphere saturated.

Without reference to the temperature, the saturation deficit gives a measure of the *dryness* of the air.

It is a distinctly more useful means of expression than relative humidity; as the following table shows:

Temperature ° F.	Relative humidity %	Saturation deficit in millibars
80	60	14·1
70	60	10·1
60	60	7·1
50	60	5·0

In each case the relative humidity is the same but the saturation deficit (i.e. the dryness of the atmosphere) increases with rise of temperature.

Evaporating power of the air (Livingston, 1932), measured by means of the Livingston-Thone white and black[1] porous porcelain atmometers (Livingston, 1915), can be correlated with temperature and saturation deficit values. Maximum evaporation occurs at the end of the long dry season, after which there is a decrease until minimum evaporation is reached in April (see Fig. 4 and Table V). Again there may be a rise in evaporation during February

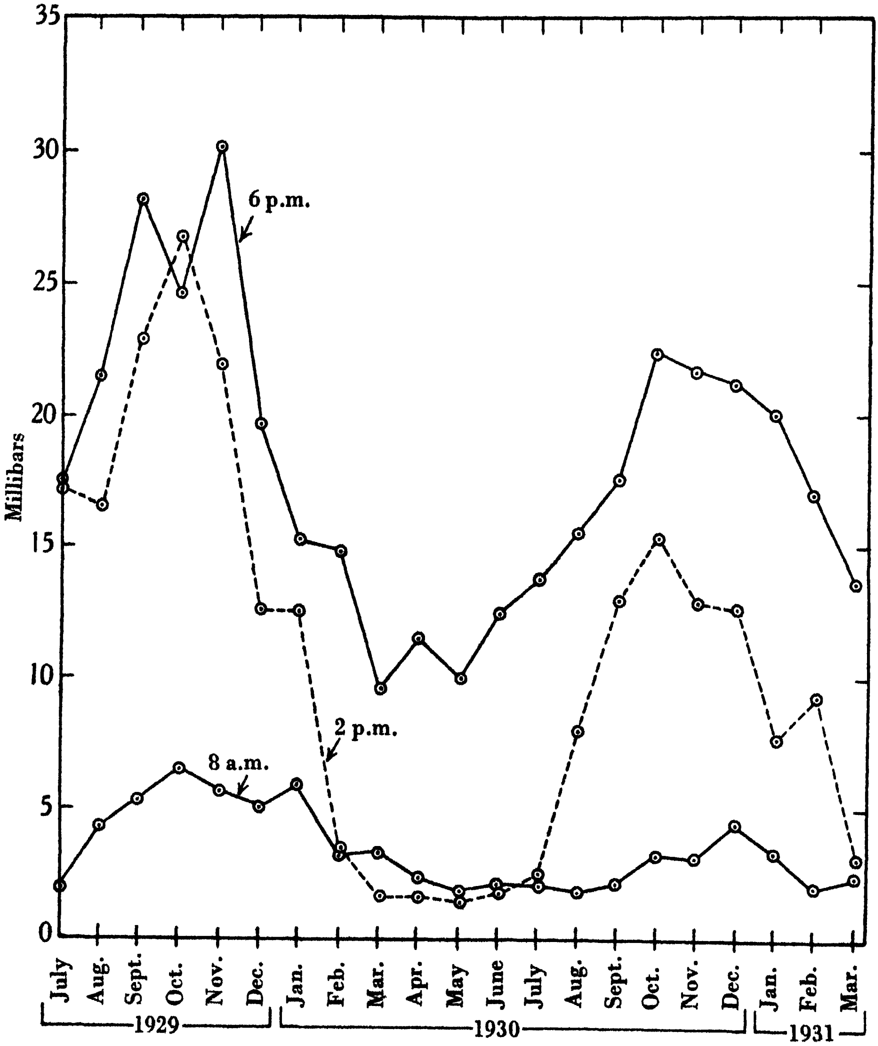

FIG. 3. Saturation deficit in millibars.

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[1] The black atmometers used were white spheres coated with celloidin lampblack, suitably standardised. Since then Livingston (1932) has recommended the use of the newly invented black porous porcelain atmometers which are proving much more satisfactory than the celloidin lampblack coated spheres.

depending on the humidity and temperature obtaining during the short dry season.

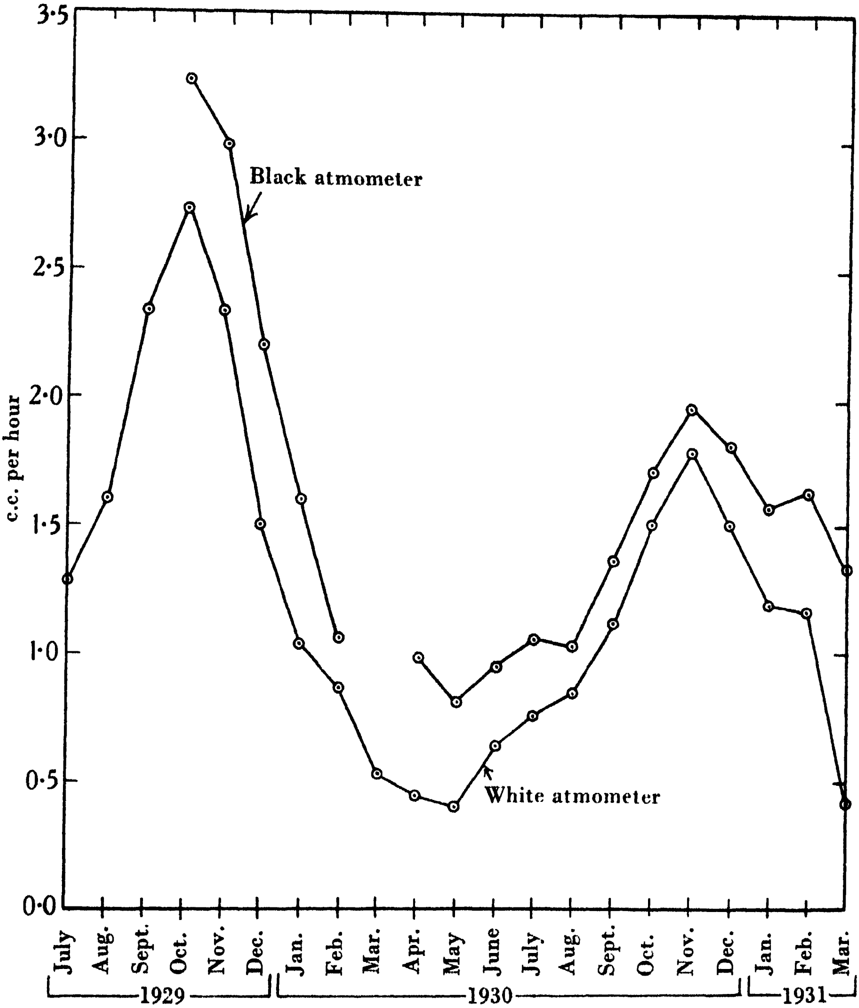

FIG. 4. Evaporation of air in c.c. per hour.

Table V. *Mean evaporation per day expressed in c.c. per hour.*

	Black atmometer		White atmometer			Black atmometer		White atmometer	
	1929–30	1930–1	1929–30	1930–1		1929–30	1930–1	1929–30	1930–1
July	—	1·05	1·27	0·76	Jan.	1·59	1·57	1·03	1·19
Aug.	—	1·02	1·59	0·84	Feb.	1·05	1·62	0·85	1·16
Sept.	—	1·36	2·32	1·11	Mar.	—	1·33	0·52	0·92
Oct.	3·22	1·71	2·72	1·50	Apr.	0·98	—	0·44	—
Nov.	2·97	1·95	2·32	1·78	May	0·81	—	0·40	—
Dec.	2·19	1·80	1·49	1·50	June	0·95	—	0·63	—

WIND.

An outstanding feature of the Kikori region is what one might term the absence of wind. The highest wind velocity over a period of 24 hours (only 5·4 m.p.h.) was recorded by means of a Robinson cup-atmometer just before the break of the first rainy season when whirlwinds or "dust-devils" were of frequent occurrence. During the rainy seasons the wind velocity is negligible, the maximum wind velocity in April, 1930, being 0·5 m.p.h.

Phillips (1930), referring to the Central Province generally, and Nash (1930), referring more particularly to the Kikori region, state that the South-East Trade winds are prevalent from May to October while, during the moist seasons, the general wind directions are either north-east or south-east. But from observations taken at 8.30 a.m. and 4.30 p.m. daily at Kikori Ecological Station over a period of 21 months, it has been found that north-east, east, and south-east winds blow throughout the year, and the proportion of north-east to east and south-east winds does not vary appreciably from month to month.

RAINFALL.

(Tables VI, VII.)

There is considerable variation in the monthly fall and annual total from year to year. This can be seen from Table VI, in which figures for the season 1928–9 have been taken from Nash's (1930) readings at Kikori Entomological Station. Although the rainfall varies considerably within short distances (Table VII gives values obtained for three stations, each about half a mile apart, over the same period), and although the rainfall recorded at Kikori Entomological Station for 1929–30 was about 4–6 in. less than that registered by the standard gauge at Kikori Ecological Station, the fall was so small in 1928–9 compared with that of 1929–30 and of 1930–1 that it is worth while including it here.

Table VI. *Rainfall in inches. Kikori Entomological and Ecological Stations.*

	Kikori Entomological Station	Kikori Ecological Station	
	1928–9	1929–30	1930–1
July	0·05	0	0·20
Aug.	0·11	0	0·01
Sept.	0·22	0	0·95
Oct.	2·25	0·65	0·32
Nov.	0·47	0·62	3·13
Dec.	3·76	6·76	4·34
Jan.	1·70	7·31	6·71
Feb.	0·50	7·89	2·38
Mar.	5·38	13·82	7·94
Apr.	5·90	11·57	6·18
May	0·65	4·73	1·92
June	0·03	0·14	0·12
Total	21·02	53·49	34·20

Table VII. *Rainfall in inches from three stations half a mile apart showing variations within short distances.*

1929–30	Station *B*	Station *E*	Station *G*
July	0	0	0
Aug.	0	0	0
Sept.	0	0	0
Oct.	0·65	0·59	1·28
Nov.	0·62	0·45	0·90
Dec.	6·76	6·15	6·31
Jan.	7·31	7·07	5·31
Feb.	7·89	6·23	6·55
Mar.	13·82	8·75	11·21
Apr.	11·57	11·57	11·93
May	4·73	3·68	4·18
June	0·14	0·11	0·07
Total	53·49	44·60	47·74

All these data on sunshine, light intensity, temperature, humidity, evaporation, wind and rainfall, collected at Kikori Standard Open Station (as contrasted with stations under canopy in different vegetation communities), show the general trend of the seasons as outlined by Phillips (1930) and Nash (1930), fairly clearly, viz.:

(1) *Long dry season*, from June to November.

(2) *First rainy season*, from November/December to February.

(3) *Short dry season* in February, except in abnormal years when there is no clear break between the first and second rainy seasons.

(4) *Second rainy season*, from late February/March to June.

OBJECTS AND METHODS OF THE INVESTIGATION.

Objects.

As stated in the introduction, the main object of the general investigation was to study the behaviour and reactions of the Tsetse fly (*Glossina morsitans* Westw.) in different vegetation communities, and to discover if possible the factors or factor complexes within those communities which made them attractive or otherwise to the fly.

Secondly it was necessary to study the succession of the different plant communities to find out whether a particular community was seral to one that was favourable or unfavourable to the fly.

Following upon this, the determination of the annual height increments of the tree seedlings, "suckers" and coppice, and the annual girth increments of the main tree species was essential in order to decide whether indigenous trees, of types found in communities unfavourable to fly, would develop fast enough in natural plant succession (if protected against fire) to be of any economic use in combating the fly.

Lastly came the study of the various soil factors with an eye to (*a*) their action on plant communities and plant succession, and to (*b*) their possible action on puparia deposited on the soils by the fly.

The objects of the investigation might be summarised as the study of:

(1) Aerial factors within various vegetation communities.

(2) Plant succession.

(3) Rate of growth of the main tree species.

(4) Soil factors.

As mentioned earlier, the purely ecological aspects of the vegetation and not of the fly will be dealt with here. The action of aerial and edaphic factors on fly activity and on the development of puparia are dealt with in other papers.

Methods.

Early in 1929 four ecological plots, each one-tenth of an acre in area, were laid out in each of six of the main plant communities at Kikori. Four plots, each one-fifth of an acre in extent, were laid out in each of the two main ecotonal communities. Two plots out of each four were fenced to exclude game, while two were left unfenced for observations upon the effects of grazing. One of the fenced and one of the unfenced plots in each community was protected against fire, while all the other fenced and unfenced plots were fired annually for observation upon plant succession and the effects of fire. There was so little game at Kikori after October, 1929, however, that no effects due to grazing could be noticed in any of the unfenced plots. For the main part, then, observations at each station were confined to the two fenced plots one of which was burned annually and the other protected throughout.

The plant communities in which plots were laid out were as follows (for nomenclature, see Phillips, 1930):

Seasonal Swamp or "*Mbuga*," *Stream bed.*	*A* 1.	Protected from fire.	*A* 2.	Burned annually.
Seasonal Swamp or "*Mbuga.*"	*B* 1.	,,	*B* 2.	,,
Ecotone. "*Mbuga*"-Acacia *spp.*	*C* 1.	,,	*C* 2.	,,
Acacia formicarum.	*D* 1.	,,	*D* 2.	,,
Acacia usambarensis.	*E* 1.	,,	*E* 2.	,,
Acacia usambarensis-Combretum-*Other spp. Ecotene.*	*F* 1.	,,	*F* 2.	,,
Combretum-*Other spp. open woodland.*	*G* 1.	,,	*G* 2.	,,
Berlinia-*Other spp. woodland.*	*H* 1.	,,	*H* 2.	,,

In December, 1929, two more fenced plots were laid out:

Upland Brachystegia microphylla.	*K* 1.	Protected from fire.	*K* 2.	Burned annually.

AERIAL FACTORS.

In each of the No. 2 plots, i.e. those burned annually and hence most like the surrounding vegetation, various instruments were placed. As the number of instruments was limited and as damaged or poor instruments had to be removed from time to time, it was not possible to instal or keep a full set of instruments in each plot.

The full set of instruments for a plot was:

A. At 48 in. above the ground (above usual height of grasses).

(*a*) In one Stevenson screen: (1) wet and dry bulb hygrometer; (2) maximum, and (3) minimum thermometers.

(*b*) In another Stevenson screen: (4, 5) bimetallic spiral thermograph and hygrograph or hair-hygrograph[1].

(*c*) In the open: (6) solar radiation thermometer (black bulb *in vacuo*); (7) grass minimum thermometer (exposed at night only)[2]; (8) Robinson cup anemometer; (9) rain gauge (5 in.)[1]; (10) black, and (11) white atmometers (Livingston spherical cup atmometers

[1] Denotes in all No. 2 plots but *A* 2 and *C* 2.

[2] Denotes in all No. 2 plots but *C* 2.

with non-absorbing valve); (12) sunshine recorder[1]; (13) Eder-Hecht photometer—readings by means of Clements' stopwatch photometer were also taken from time to time[2].

B. At 6 in. above the ground (i.e. below level of grasses, etc., except just after the fires): (15) grass minimum thermometer; (16) black, and (17) white atmometers.

C. In four of the No. 1 plots (*B* 1, *D* 1, *G* 1, and *H* 1), a few instruments were placed at 6 in. above the ground. These instruments were: (1) grass minimum thermometer, (2) white atmometer for comparison with 6 in. instruments in No. 2 plots, and (3) solar radiation thermometer.

Instruments in the No. 2 plots were read twice daily (except Sunday when readings were taken in the morning only) between 7.30 and 9.30 a.m. and 3.30 and 5.30 p.m. These readings were begun on July 1st, 1929, and carried out until September 30th, 1930. Shortage of staff then necessitated removal of instruments from Plots *A*, *C*, and *F*, and the reading of the instruments in all the other plots once daily, in the morning, only.

SUCCESSION.

In each of the plots a quadrat of 4 sq. m. was laid out and the position of each individual plant was marked on a quadrat chart. Quadrats were re-charted at yearly intervals. Besides the quadrat, fifteen analysis circles each of 1 sq. m. were set out in each plot. The different species occurring in each circle were listed annually.

Phenological observations were made twice a week on each plot. Fairly full data were obtained as to height of grass and other ground flora, flowering, setting of seed, shedding of seed and drying up of plants. Similarly, observations were made upon tree species at each plot—first leaves, full foliage, first flowers, full flower, first fruits, full fruit, dropping of leaves, shedding of seed and entire defoliation (see p. 225, and Table X, p. 226).

A belt transect, 300 ft. long by 10 ft. wide, was laid out in *Berlinia* woodland, and protected from fire, in the second rainy season, 1930. The positions of all woody plants in the transect were charted. The transect was re-charted in the second rainy season, 1931.

As the quadrats and analysis circles were not done by the writer, he is not able to discuss the results in this paper. He is confining his remarks to, and drawing his conclusions from, observations made in the transect and phenological work.

RATES OF GROWTH.

(*a*) *Girth increments.* About 1100 trees of twenty-three of the principal species were banded, where possible at breast height. This was however not always possible owing to difference in size and shape of the trees. Individual trees ranged from very small to amongst the largest in each species. Measurements were made at the base of the band at the end of the long dry season in 1929. The trees were re-measured after the interval of one year.

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[1] Denotes in *B* 2, *F* 2, *G* 2, *H* 2 and later, *K* 2 only.

[2] Denotes in *B* 2 and *H* 2 only.

(*b*) *Height increments.* In each of the plots protected against fire, seedlings, suckers and coppice (burned back seedlings) were marked with numbered wire pegs. About 1400 seedlings, suckers and coppice of eighteen species were staked and measured during the second rainy season, 1930. They were measured again during the second rainy season, 1931.

SOILS.

The programme for the study of soil factors was confined more or less to the purely physical factors. These can be grouped as follows:

(*a*) Factors varying within short intervals: (1) temperatures at different depths; (2) water content; (3) water-supplying power of the soil.

(*b*) Factors varying with the seasons: (1) permeability; (2) porosity; (3) organic content; (4) *p*H.

(*c*) Factors varying very little from season to season and taken to be more or less constant: (1) maximum water-retaining capacity; (2) hygroscopic coefficient; (3) maximum shrinkage of soils; (4) colloid content.

(*a*) (1) *Temperature.* In each of the No. 2 plots, soil thermometers were placed at the surface and at depths of 1 and 5 ft. These were read at the same time as the various instruments registering aerial conditions. In addition, data were obtained in certain plots for maximum and minimum surface temperatures.

(2) *Water content.* From January, 1930, to March, 1931, samples were taken in duplicate each week for each of the No. 1 and No. 2 plots at the surface and at a depth of 1 ft. The total holard was determined by the oven-drying method. In addition, notes were taken daily on "state of ground," i.e. as to whether the soils were inundated, wet, moist, dry or cracking, in order to obtain some idea of the water content of the soils at the point at which they cracked.

(3) *Water-supplying power of the soil.* Livingston porous porcelain soil points (Livingston and Koketsu, 1920) were employed in duplicate for the determination of the water-supplying power of the various soils at 0–1 in. Only a limited number were available, so it was not possible to take observations at varying depths. As a rule, the soil points were placed in the soil for a period of 24 hours.

(*b*) (1) *Permeability.* This factor was measured by the steel tube method of Burger (1923). Determinations were made in 5-plicate at depths of 0–10 and 10–20 cm. during the long dry and second rainy seasons. A cylindrical steel tube, with a cross-section of 100 sq. cm. and a depth of 20 cm. having a bevelled edge at one end and marked at 10 cm. from either end, was used. The tube was placed with the bevelled edge upon the ground, a block of wood was laid across the other end and gently tapped with a hammer until the 10 cm. mark was flush with the surface of the ground. There was then 1 litre of soil in the tube below the soil surface. A litre of water was poured into the tube and the time, from the pouring of the water till the disappearance of the last drop into the soil, was taken by means of a stop watch.

(2) *Porosity.* This was calculated from the determination of the real and apparent specific gravities of the soil as outlined by Emerson (1925, pp. 23–31).

Apparent specific gravity was determined as follows. Duplicate samples were taken in cylindrical brass tubes of 50 c.c. capacity. The tube has a bevelled edge at one end and a perforated brass cap which will fit over the other end. The cap is removed and the tube driven into the ground by placing on it a block of wood and pressing down with one's weight until the upper end of the tube is flush with the surface of the soil. The whole tube is then undercut and removed with the soil in it. The cap is put on the upper end and the whole inverted. The soil is cut level with the bevelled edge of the tube by drawing a taut wire across the end of the tube. The tube then contains 50 c.c. of soil in its natural make-up. The sample is air-dried and weighed.

$$\text{Apparent sp. gr. of the soil} = \frac{\text{Wt. of 50 c.c. of soil}}{\text{Wt. of an equal vol. of water}}.$$

The same samples are used for determining the real specific gravity of the soils. A specific-gravity bottle of known weight is half filled with water and weighed. About 10 gm. of soil are added and the weight is again determined. The water in the bottle is then raised to the boil to drive off any air in the soil and, after cooling, enough water is added to fill the bottle, which is then weighed. The weight of the bottle full of distilled water only is determined. From these determinations the actual weight of the soil used and the weight of the water which it has displaced can be calculated.

$$\text{Real sp. gr. of the soil} = \frac{\text{Wt. of soil used}}{\text{Wt. of water displaced}}.$$

$$\text{Porosity} = \frac{\text{Real sp. gr.} - \text{apparent sp. gr.}}{\text{Real sp. gr.}}.$$

(3) *Organic content.* The incineration method described by Emerson (1925, p. 40) was used in these determinations. This method is known to give rather high values and those obtained at Kikori do appear rather high. Determinations were carried out as follows: some of the soil sample which has previously been oven-dried is tested for the presence of carbonates by means of HCl. If a carbonate is present, a definite weight of the soil is treated with HCl and, after all effervescence has ceased, the liquid is filtered off and all the soil is washed on to the filter paper. It is washed until the washings show no trace of acid. The soil is then oven-dried and weighed. The loss in weight is the weight of the carbonates removed.

If no carbonate is present the step just described is omitted. The soil with carbonates either absent or removed is then placed in a crucible and heated to a red heat at which it is maintained until all the organic matter has been burned off. It is cooled in a desiccator and weighed. The difference between the second and third weighings is the weight of the organic matter. This is calculated as a percentage of the weight of the original oven-dried soil.

(4) p*H*. The "Hellige" disc comparator and the Wherry double-edge comparator (Wherry, 1924) were employed, but the two sets of indicator solutions did not keep well. The two comparators, as a result, gave entirely different readings with the same solutions, and all results of *p*H work done at Kikori had to be discarded.

A number of well air-dried soil samples from certain of the plots at Kikori, however, were sent to the writer by Mr G. W. St Clair Thompson. Determinations of the *p*H of these samples were made electrolytically by Mr B. Segal, of the Department of Chemistry at the University of the Witwatersrand, to whom the writer is very grateful. These results have been used in this paper.

(*c*) (1) *Maximum water-retaining capacity*, referred to hereafter as M.W.R.C. Soil samples were taken in brass boxes in the same way as described for the determination of the apparent specific gravity of soils. The boxes were placed in shallow troughs and water was added to within 1 mm. of the top of the boxes. After 24 hours the boxes were removed, placed upon a slope and allowed to drain for an hour. The outside of each box was then rapidly dried and the box and its contents weighed. The box and soil were dried in a steam oven, cooled in a desiccator and re-weighed. The difference in weight is equal to the weight of the maximum amount of water that can be held by the weight of the soil used. It is calculated as a percentage of the weight of soil used.

This method is outlined by Bates and Zon (1922), and is an improvement of Hilgard's method (1907).

(2) *Hygroscopic coefficient*[1]. Soil samples were sifted, thoroughly air-dried and carefully weighed in quantities of about 10 gm. These were placed in shallow metal trays to a depth of 1 mm. in hygroscopicity boxes for 24 hours.

A hygroscopicity box is a wooden box with internal dimensions of 12 × 9 × 8 in. The internal surfaces are thoroughly covered with thick parawax-petroleum to prevent absorption and warping. The lid is air-tight and the internal surfaces are also covered with wax. In the bottom of the box, water is placed to a depth of 3 in. and the walls of the box above the water are lined with blotting paper to ensure rapid dissemination of water vapour. Two inches above the water are wires from wall to wall, holding the metal trays, which are 7 × 5 × 0·75 in.

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[1] The *hygroscopic coefficient* of each soil was determined because the *wilting coefficient* could be calculated from the values obtained. According to the work of Briggs and Shantz (1912), the wilting coefficient of a soil can be obtained by means of the following formula:

$$\text{Wilting coefficient} = \frac{\text{hygroscopic coefficient}}{0{\cdot}68 \pm 0{\cdot}012}.$$

The box is kept at a constant temperature in a concrete cupboard for the 24 hours of the experiment. At the end of that time, the soil is removed rapidly to weighing bottles and weighed, dried in a steam oven and weighed again.

The hygroscopic coefficient is the difference between the weight of the soil after being in the almost saturated atmosphere for 24 hours and its oven-dry weight, calculated as a percentage of the oven-dry weight.

The criticisms of Keen (1931) as to the meaning and difficulties of determination of the hygroscopic coefficient are known but, despite this, it is held that the determination can be carried out satisfactorily if care be taken to avoid sudden changes in temperature.

(3) *Maximum shrinkage of soils.* Samples were taken by means of the brass boxes described above. The box was allowed to stand in water till the soil was saturated and then allowed to drain for an hour. The surface of the saturated soil was then scraped even with the top of the box which was placed in a steam oven. After drying and cooling the soil, the cracks were filled with mercury and the amount of mercury necessary was measured volumetrically. The volume of the saturated soil was 50 c.c. (volume of the brass box) and the volume of mercury used was calculated as a percentage of the volume of the saturated soil.

(4) *Total colloid content.* The total percentage of colloids in the soils was determined by means of the Bouyoucos colloid hydrometer (Bouyoucos, 1927).

50 gm. of air-dried soil are placed in a mortar; enough distilled water to make a paste is added and the mass is pestled vigorously for 5 min. Enough water to make a thin suspension is added and this is well stirred. It is allowed to stand for half a minute, when the supernatant liquid is poured into a special large cylinder. The paste is then pestled vigorously again for 5 min., water to make a thin suspension is again added and, after stirring, allowed to stand for half a minute. The same procedure as before is followed, and this is repeated until all the clays are dispersed, the liquid becoming more or less clear after stirring.

5 c.c. normal KOH are then added to the liquid in the cylinder and water is added to make it up to 1130 c.c. The liquid is stirred vigorously for 1 min., the hydrometer is placed in it and it is allowed to stand for 14½ min. (timed by a stopwatch). The hydrometer is then tapped gently to obviate "lag" and, at the end of another half-minute (15 min. from placing the hydrometer in the liquid), the reading is taken. The reading is in gm. per litre and this amount, divided by the weight of the soil used, equals the percentage of colloid in the liquid.

The temperature of the liquid is taken and the following correction applied to the percentage colloids. All readings are reduced to a basis of 67° F., 1° F. change being equivalent to a change of 0·35 per cent. in the colloids. For temperatures above 67° F. the values are added, for temperatures below, the values are subtracted.

This method does not give an impression of the *state of activation* of the colloids of various kinds. All it does is to record the *total colloids.*

Soil types are determined roughly from the total percentage colloid as follows:

Up to 10 per cent. colloids	... ...	Sands.
10–20 „ „	... ...	Sandy loams.
20–30 „ „	... ...	Loams.
30–50 „ „	... ...	Clay loams.
50–75 „ „	... ...	Clays.
Over 75 „ „	... ...	Heavy clays.

The above outline covers the programme and methods of work fairly fully. The results obtained are given in the following sections.

SYNECOLOGICAL TERMS USED.

The following terms, most of which were originally introduced by Dr F. E. Clements, are used in this paper:

Sere. A unit plant succession, comprising the development of a formation from the pioneer stage to the climax.

Hydrosere. The sere commencing in water or moist sites.

Xerosere. The sere commencing upon dry sites—rocks, dry soil.

Community. A general term applied to any aggregation of plants irrespective of its rank.

Consocies. A seral community with a single dominant.

Associes. A seral community with two or more dominants.

Seral. Developmental, not climax.

Climax. In equilibrium with the environment, fixed (relatively).

Sub-climax. A seral community simulating a climax on account of its further development being inhibited by some disturbing factor such as fire.

THE CHIEF COMMUNITIES.

A. THE "MBUGA" STREAM-BED COMMUNITY.

Soils.

The soils are alluvial, belonging to the so-called "black cotton" type. Except for a superficial layer of decaying vegetable matter, 1–3 in. thick, seldom affected by the fires which sweep the country annually, the soils are rich in clay. The total colloid content ranges from 45 per cent. at the surface to over 50 per cent. at a depth of 1 ft. This would define these soils as clay loams or clays.

The M.W.R.C.[1] and hygroscopic coefficient are high. The latter does not vary much from the surface to 1 ft. depth, being about 15 per cent. throughout, but the latter ranges from over 100 per cent. at the surface to 40 per cent. at a depth of 1 ft.

The soils are slightly alkaline, having a pH of just over 7, with practically no change from the surface to 1 ft. depth. The organic content is very high, ranging from 20 to 25 per cent. at the surface to 10 per cent. at the depth of 1 ft.

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[1] See p. 192.

During the second rainy season the soils are inundated by a flowing stream to a depth of 6-12 in. with the result that the water-supplying power (W.S.P.) of the soil and the holard are at a maximum. At the end of the long dry season the soils may be very much cracked, the total possible shrinkage of the soil ranging from 40 per cent. at 12 in. to 55 per cent. at the surface. After heavy rainy seasons, however, the total holard either at the surface or below may not fall below 30 per cent. and the soils may still be quite impermeable at the end of the dry season.

The porosity of the soils varies in the dry and wet seasons. During the wet seasons it is found to be about 0·5 at 1 ft. and 0·5–0·6 at the surface while, during the dry seasons, it increases to 0·55 at 1 ft. and 0·7 at the surface.

During the dry season, especially after the fires have occurred, high surface temperatures (140–150° F.) are registered at midday. The temperature of the soil at 1 ft. below the surface lags 6-8 hours behind that of the surface soil, while that at 5 ft. lags 3 5 days behind that at 1 ft. The annual range in temperature at 1 ft. is 62-79° F. while at 5 ft. it is 65-76° F.

During the long dry season and the first rainy season the temperatures at 1 ft. are higher than those at 5 ft. After that, the temperature at 1 ft. drops below that at 5 ft. until the middle of the next long dry season.

Aerial conditions.

The temperatures at this station rise and fall with the seasons, as already outlined for the standard station. The highest absolute maximum recorded was 94·25° F. during November, 1929. The lowest minimum was 38·25° F. in August, 1929.

Maximum solar radiation temperatures range from 132° F. in the rainy seasons to 162° F. in the long dry season.

After the fires the grass minimum thermometer at 6 in. above the soil registers temperatures lower by 2-4° than that at 48 in. This continues until February when the vegetation has again sprung up and has completely overshadowed the lower instrument. Lowest temperatures from the grass minimum thermometers (for which, prior to October, 1929, there are no readings) were registered in July, 1930, the lowest at 6 in. being 40° F. and at 48 in. 38° F.

Livingston-Thone black and white atmometers give rather interesting figures for the evaporating power of the air. The evaporation from the white bulbs at 6 and 48 in. above the ground is more or less proportional throughout the year, the atmometer at 48 in. evaporating about 0·5 c.c. per hour more than that at 6 in., except in the middle of the second rainy season when the difference is rather greater. At the end of the long dry season, the evaporation from the black bulb at 48 in. is very much greater than that from the white bulb at the same height, the difference in October being 1·4 c.c. per hour.

After that, however, the difference decreases and, during the rainy seasons, the difference between the two remains about 0·5 c.c. per hour.

The most striking results are those registered by the black atmometer at 6 in. above the soil surface. After the fires at the end of the long dry season when the soil is bare, black, and wind swept, and when radiation is high the evaporation from the black bulb at 6 in. is higher than that from the black bulb at 48 in. As the soil surface becomes covered with vegetation the evaporation from the lower black bulb decreases till in February it is lower than that from the white bulb at 48 in. The highest mean evaporation per hour is obtained in October and the lowest in April.

The evaporation in c.c. per hour (monthly mean) for the four atmometers in October 1929 and April 1930 was:

	Black (48 in.)	White (48 in.)	Black (6 in.)	White (6 in.)
Oct. 1929	4·06	2·85	4·25	2·61
April 1930	0·88	0·42	0·24	0·13

A rain-gauge, placed under the vegetation at a height of 6 in. from the ground to find interception loss, recorded 16·24 in. less than a gauge at 48 in. above the ground, 50 yards away, in 1929–30, and 6·99 in. less in 1930–1.

Vegetational features.

The seasonal aspects of the vegetation are most interesting. First one and then another species is the dominant for a time. After the first rains following upon the annual fires, grasses and *Cyperus* spp. make their appearance. *Digitaria scelaria*, a small grass, is usually the first to flower and to become dominant. It is superseded by *Panicum maximum* and *Cyperus* spp., which gradually reach a height of 160 cm. A species of *Aspilia*, a yellow Composite, eventually becomes dominant. It begins flowering at a height of 80 cm. in February, and by April the plants are up to 250 cm. in height, some in flower and some setting seed. *Hibiscus cannabinus* and *Sesbania* sp. appear in flower in April at heights of 250–300 cm. Smaller herbs which are seen in flower during the year are *Phyllanthus* sp., *Crotalaria* spp., *Acalypha* sp., *Tragia* sp., *Asclepias semilunata* and *Dolichos* sp. Of these, the small yellow-flowered, climbing *Dolichos* is the most important. It appears when the grasses are in full flower in February and gradually climbs up the various plants until it suppresses all the weaker and younger ones, reaching a height of 150 cm. and finally becoming co-dominant with the *Aspilia*. By June all the grasses have shed their seeds, *Sesbania* is defoliated and most of the other herbs have finished fruiting. A few *Aspilia*, *Cyperus* and *Dolichos* may still be in flower or setting seed. In July all the plants have shed their seeds and all the vegetation begins to turn yellow and dry.

Phot. 1. Plot A 2 during the Dry Season after the fire
Acacia campylacantha behind

Phot. 2 Plot A 2 during the second Rainy Season.

SCOTT—TANGANYIKA COMMUNITIES

B. SEASONAL SWAMP ("MBUGA") COMMUNITY.

Soils.

The soils are very like those described for the "*Mbuga*" *Stream Bed*, being clays with a colloid content ranging from 50 per cent. at the surface to 60 per cent. at a depth of 1 ft.

The M.W.R.C. and hygroscopic coefficient are high. The former ranges from 80 per cent. at the surface to 40 per cent. at 1 ft. depth and the latter from 15 per cent. at the surface to 18 per cent. at 1 ft. The organic content is very high, being about 15 per cent. at the surface and 10 per cent. at the lower depth. The soils are alkaline with a *p*H of just over 7.

During the middle of the second rainy season, the soils are inundated by a flowing stream to a depth of several inches, so that here too, at this period, the holard and W.S.P. of the soil are at a maximum. At this period the surface holards may be 60-100 per cent. while those at 1 ft. keep fairly constant at 35–45 per cent. At a time when the surface holard has dropped to 40–50 per cent., the W.S.P. of the soil, measured by means of the Livingston soil point, is 0·17–0·22 gm. per hour.

As the soils dry up, they begin to crack. Their total possible shrinkage is 42 48 per cent. and, as they may dry to a holard of 2 per cent. at the surface with a W.S.P. of 0·0005 gm. per hour, and to 17 per cent. in the subsoil, the amount of cracking is very great. It was noticed that the holard of the surface soils, when cracks first appeared, was 43–45 per cent. This cracking makes a great difference to results obtained in determinations of the permeability and porosity of soils at different seasons. During the rainy seasons the soils are inundated and impermeable, with a porosity of 0·5. During the long dry season, when porosity is 0·6, 1 litre of water will disappear into 1000 c.c. soil at 0–10 cm. in 30 sec., and into 1000 c.c. soil at 10-20 cm. in 4 min.

High surface temperatures (120–150° F.) are recorded after the vegetation cover has been burned. Temperatures of the 1 ft. soil thermometer lag 6–8 hours behind the surface soil temperatures and those of the 5 ft. thermometer lag about 60 hours behind those of the 1 ft. thermometer. The range in temperature of the 1 ft. thermometer over a year is 65-83° F. and of the 5 ft. thermometer 67–77° F. The 1 ft. thermometer registers lower temperatures than that at 5 ft. from March to August, but for the rest of the year it shows higher temperatures.

Aerial conditions.

The seasonal variations in temperature, humidity, evaporation, sunshine, light and rainfall have already been described (pp. 179–87) as that of the standard plot.

The highest absolute maximum temperature obtained was 91·75° F. and the lowest minimum was 38·5° F. Maximum solar radiation temperatures ranged through the seasons from 146 to 160° F.

Here, too, the grass minimum thermometer at 6 in. records lower temperatures than that at 48 in. while the grass cover is short after the fires. The lowest grass minimum temperatures ever recorded at Kikori, 33·25° F. in July and 35·50° F. in August, 1929, were at 6 in. when the 6 in. grass minimum thermometer, unfortunately, was the only thermometer of its kind on the station so that there was none at 48 in. for comparison. In July, 1930, the instruments at both levels recorded minimum temperatures of 38° F.

The highest mean monthly sunshine was 7·3 hours per day and the lowest was 2·7 hours per day.

The greatest mean light value for any month in the year was 0·076 Bunsen Roscoe units per second, and the lowest monthly mean was 0·021 Bunsen Roscoe units per second.

The winds recorded here were the highest recorded in any community at Kikori, but the highest value per hour over 24-hour periods was only 5·4 m.p.h. in October, 1929.

The evaporation from black and white atmometers at 48 and 6 in. is similar to that in plot *A* (Mbuga stream-bed community). During the dry season, after the fires, there is not much difference between the evaporation from the two black atmometers. Then that from the black bulb at 6 in. drops below that at 48 in., which shows the highest evaporation for the rest of the year. The 6 in. black atmometer readings drop below those of the white atmometer at 48 in. for most of the year and keep just above those of the white atmometer at 6 in. The highest mean evaporation per hour (monthly mean) was obtained in October and the lowest in April. The evaporation in c.c. per hour (monthly mean) for the four atmometers in October, 1929, and April, 1930, was:

	Black (48 in.)	White (48 in.)	Black (6 in.)	White (6 in.)
Oct. 1929	3·22	2·72	3·22	2·49
April, 1930	0·98	0·44	0·32	0·17

The rainfall registered by a gauge at 4 ft. in this plot was 53·4 in. in 1929–30 and 34·20 in. in 1930–1.

Vegetational features.

The most numerous plants in this community are *Digitaria scelaria, Ischaemum* sp., *Panicum maximum, Cyperus* spp., *Dolichos* sp., and *Aspilia* sp. Less numerous are species of *Indigofera, Tragia* and *Corchorus*, and *Hibiscus cannabinus*, while only a few of the following occur: *Anthephora* sp., *Echinochloa haploclada, Pennisetum massaicum, Rottboellia exaltata, Setaria Holstii, Sorghum versicolor, Crotalaria* spp., *Cleome monophylla* and species of *Sesbania, Acalypha, Phyllanthus, Achyranthes* and *Commelina.*

Seasonal aspects are as follows: after the beginning of the rains, grasses, *Cyperus* spp. and *Aspilia* sp. make their appearance. By December grass blades are about 60 cm. high and flowers of *Setaria Holstii* and *Panicum* *maximum* are numerous at a height of 100 cm. The last-named is dominant for a time. These are followed by *Ischaemum*, *Digitaria scelaria*, *Echinochloa haploclada*, *Commelina* sp., *Cleome monophylla* and *Sesbania* sp. By March the grasses are much matted by *Dolichos* which suppresses most of the smaller annuals. At this time, most of the grasses (*Panicum maximum*, *Echinochloa haploclada*, *Setaria Holstii*, *Ischaemum* sp. and *Rottboellia exaltata*), at a height of 150 cm. are in full flower or are setting seed. *Hibiscus cannabinus*, *Sesbania* sp. and *Aspilia* sp. are in full flower at heights ranging from 200 to 400 cm., and *Dolichos*, climbing up other plants, appears in flower.

After most of the grasses have finished flowering, *Sorghum versicolor* comes into flower. By the end of May most of the grasses have shed their seed, and *Aspilia*, *Dolichos*, *Hibiscus cannabinus* and *Sesbania* are in fruit, though *Aspilia* and *Dolichos* may continue flowering until July. The grasses and other plants, with the exception of *Aspilia*, gradually dry or turn yellow and, by the end of October, all the vegetation is dry enough to burn.

C. ECOTONE OF "MBUGA"-*ACACIA* spp.

Soils.

The soils are alluvial and closely resemble those of the "Mbuga." The colloid content is about 45 per cent. at the surface and ranges from 50 to 56 per cent. at 1 ft. depth. The M.W.R.C. is very much lower than in the two previous types with which we have dealt, but the hygroscopic coefficient is still high. At the surface the M.W.R.C. is 40–50 per cent. and at 1 ft. is only 30 per cent. The hygroscopic coefficient ranges from 14 per cent. at the surface to 17 per cent. at 1 ft. The organic content of the surface soil is about 16 per cent. while that of the subsoil is 10 per cent.

Here, too, the soils are inundated during the second rainy season, when maximum holards of over 100 per cent. at the surface and of 46 per cent. at 1 ft. are obtained. At the end of the dry season holards as low as 3 per cent. at the surface and 12 per cent. at 1 ft. are reached. Shrinkage of the soil ranges from 38 per cent. at the surface to 30 per cent. in the subsoil, and consequently cracking takes place as the soils dry.

During the rainy seasons the soils are impermeable, and have a porosity of 0·52 at the surface and 0·46 at 1 ft. During the dry season when the soils are much cracked, the permeability is great, 1 litre of water disappearing into 1000 c.c. soil at 0–10 cm. in 0·5 min., and at 10–20 cm. in 1–2 min. The porosity in the dry season is 0·58 at the surface and ranges from 0·59 to 0·62 in the subsoil.

High surface soil temperatures (140–150° F.) occur here during the long dry season after the fires. The 1 ft. soil temperatures lag 6–8 hours behind those of the surface soil, while the 5 ft. temperatures lag as much as 6 days behind those at 1 ft. The range in mean monthly temperatures at 1 ft. is 64–83° F. and at 5 ft. is 69–79° F.

As in the other soils, already described, temperatures at 1 ft. were lower than those at 5 ft. from March to July but were higher for the rest of the year.

Aerial conditions.

The conditions appear to be rather more severe in this plot in that the wind is cut off by the trees to some extent, and the actual canopy is so light that there is very little, if any, reduction in radiation.

The absolute maximum temperature in this plot was 95·25° F. and the absolute minimum was 38·5° F. Maximum solar radiation temperatures ranged from 138 to 162° F. The relative light intensity at 4 ft. in bright sun at midday ranges from 100 per cent. in the open to 40 per cent. under canopy of *Acacia Seyal.*

The evaporation in this community is not so high as that in the others already described, due probably to there being less wind. Although the 6 in. black atmometer records fairly high evaporativity, at no time is this higher than that recorded by the corresponding instrument at 48 in. The readings of the 6 in. black atmometer are higher than those of the 48 in. white atmometer for several months, but are somewhat lower during the rainy months and during the first part of the long dry season. The 6 in. white atmometer records the lowest evaporativity of all throughout the year.

Mean monthly evaporation in c.c. per hour for October and April are:

	Black (48 in.)	White (48 in.)	Black (6 in.)	White (6 in.)
Oct. 1929	3·04	2·38	2·91	2·20
April, 1930	0·91	0·44	—	0·26

The rain-gauge in this plot, although having no overhead canopy and although less than 100 yards from the standard gauge, recorded 4·72 in. rainfall less than that gauge in 1929–30 and 2·19 in. less in 1930–1.

Vegetational features.

This community consists of a consocies of *Acacia Seyal* Del. (without galls). Other species occurring in the community are *Ac. Seyal* var. *fistula* Oliv. (with galls), *Ac. verugera* and *Ac. campylacantha.* The trees are fairly widely spread (5–15 m.), have upright boles, and with the exception of *Ac. campylacantha* and *Ac. verugera* have very sparse foliage. As a result the shade cast at any time of the year is but slight.

The most numerous of the grass-herb ground flora are *Anthephora* sp., *Ischaemum* sp., *Aspilia* sp., *Acalypha* sp. and *Phyllanthus* sp. Other plants occurring are *Digitaria horizontalis, Echinochloa haploclada, Panicum maximum, Setaria Holstii, Setaria equatorialis, Sorghum versicolor* and *Themeda triandra*; *Cyperus* sp.; *Cassia* sp. (small herb), *Crotalaria* spp., *Dolichos* spp., *Indigofera* sp., *Sesbania punctata* and *Tephrosia* sp.: also *Achyranthes* sp., *Cleome monophylla*, *Commelina* sp., *Convolvulus* sp., *Corchorus* sp., *Hibiscus cannabinus*, *Oldenlandia* sp., *Polygala* sp., *Euphorbia* sp. and *Tragia* sp.

After the fires, the first species in flower are *Setaria Holstii* and *Anthephora* sp., followed by *Digitaria horizontalis* and *Themeda triandra*. The *Anthephora* is the most numerous. The next in flower are *Setaria equatorialis* and *Ischaemum*, with the herbs *Crotalaria* spp., *Aspilia* sp., *Acalypha* sp., *Hibiscus cannabinus* and *Tragia* sp. *Ischaemum* is the dominant member of the ground flora for a while. By April most of the grasses have set seed and *Aspilia* sp., *Hibiscus cannabinus*, *Sesbania* sp. and *Sorghum versicolor* are in flower at 200–300 cm. By the end of May these, too, are setting seed, and by July all with the exception of *Aspilia* sp. are dry and yellow.

D. CONSOCIES OF *ACACIA FORMICARUM* Harms (BLACK GALL ACACIA, FLÖTENAKAZIE.)

Soil.

This is another of the "Mbuga" type of alluvial soils with a colloid content of 40 per cent. at the surface and 47–56 per cent. at 1 ft.

The M.W.R.C. is rather lower here than in the "Mbuga" but not very much lower than in the "Mbuga" ecotone. It ranges from 36 to 41 per cent. at the surface to 26 29 per cent. in the subsoil. The hygroscopic coefficient ranges from 7 to 11 per cent. at the surface to 14 per cent. at a depth of 1 ft. The organic content at the surface is 12 per cent. and in the subsoil from 7 to 10 per cent.

During the rainy seasons the soils are very wet and occasionally may be inundated. Holard values may reach 67 per cent. at the surface and 42 per cent. in the subsoil during the rainy seasons, and values as low as 2 per cent. at the surface and 7 per cent. in the subsoil may be obtained in the dry season. With a surface holard of 30 per cent., the W.S.P. of the soil at 0–2 in. was found to be 0·18–0·19 gm. per hour. With a holard of 6 per cent. at the same depth, it was found to be less than 0·001 gm. per hour.

Shrinkage of the soil varies from 10 to 20 per cent., but cracking during the dry season is very marked indeed. Cracking is found to occur first when the holard approximates 30 per cent.

During the rains the soils are impermeable, and even during the dry season they are not very permeable, a litre of water taking 16–20 min. to disappear into 1000 c.c. of soil at 0–10 cm. and 23 min. at 10–20 cm. depth.

Porosity does not vary much from season to season, being about 0·5 at the surface and 0·4 in the subsoil.

Surface soil temperatures are not as high as those recorded for the soils with which we have already dealt, 131° F. being the highest recorded in a year. The range in temperature at 1 ft. is 67–84° F. and at 5 ft. is 71–79° F.

The 1 ft. temperature shows a lag of 6–8 hours behind that at the surface and the 5 ft. temperatures lag 2–4 days behind those at 1 ft. (Fig. 5).

Aerial conditions.

The temperature ranges in this community are wide. Here, too, the trees cast very little shade but cut down the wind appreciably. The highest absolute maximum temperature recorded on this plot was 94·5° F. and the lowest minimum was 37·0° F.

Maximum solar radiation temperatures were high, the mean monthly maxima being over 140° F. for at least 8 months in the year and the highest absolute maximum being 164° F.

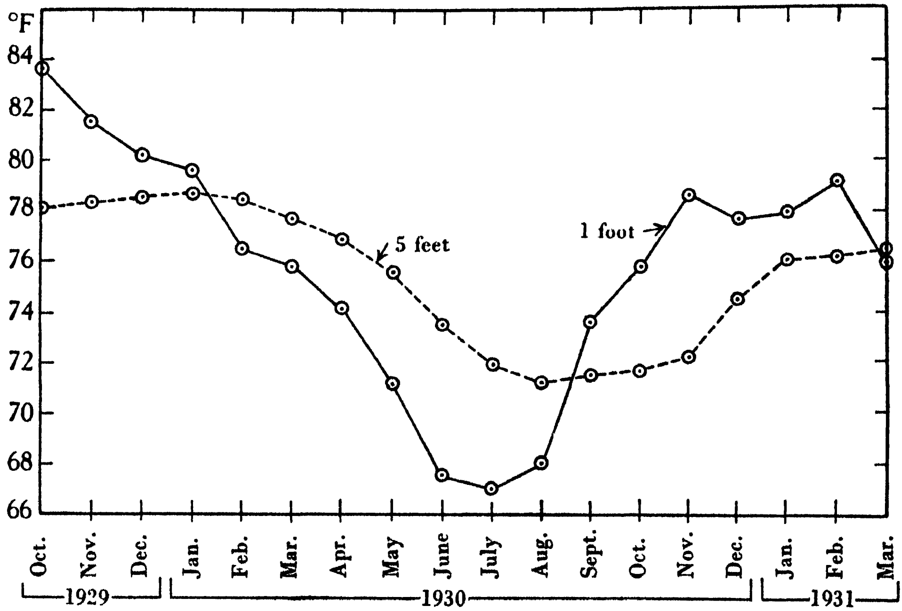


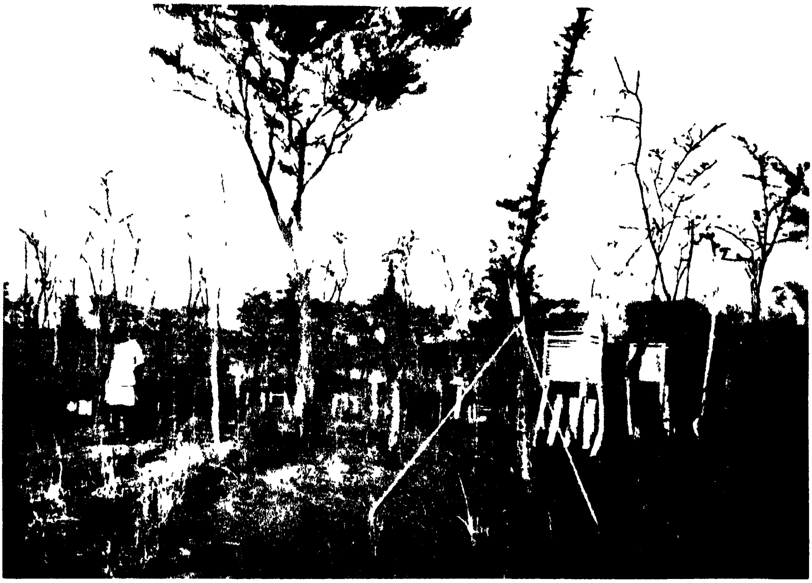
FIG. 5. Contrast of soil temperatures at 1 ft. and 5 ft. in plot *D* 2 (typical).

The lowest grass minimum temperature at 48 in. was 36° F. and at 6 in. was 37° F. For a month or two after the fires, when no grass cover is present, the grass minima at 6 in. are lower than those at 48 in. but, for the rest of the year, lower temperatures are recorded by the latter.

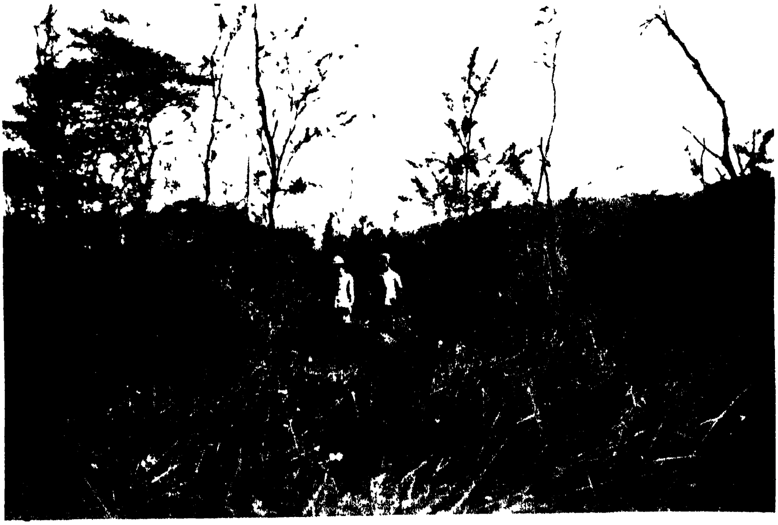
Relative light intensity at midday on bright sunny days varied from 30 to 70 per cent. under canopy.

The wind values were low. The highest mean velocity over 24 hours of 3·07 m.p.h. was recorded after the fires at the end of the dry season. The maximum wind in April (mean over 24 hours) was only 0·36 m.p.h.

For a short period after the fires, the evaporation from the black atmometer at 6 in. is a good deal higher than that from the 48 in. instrument, but it decreases with the advent of the rains until it is well below that of the white

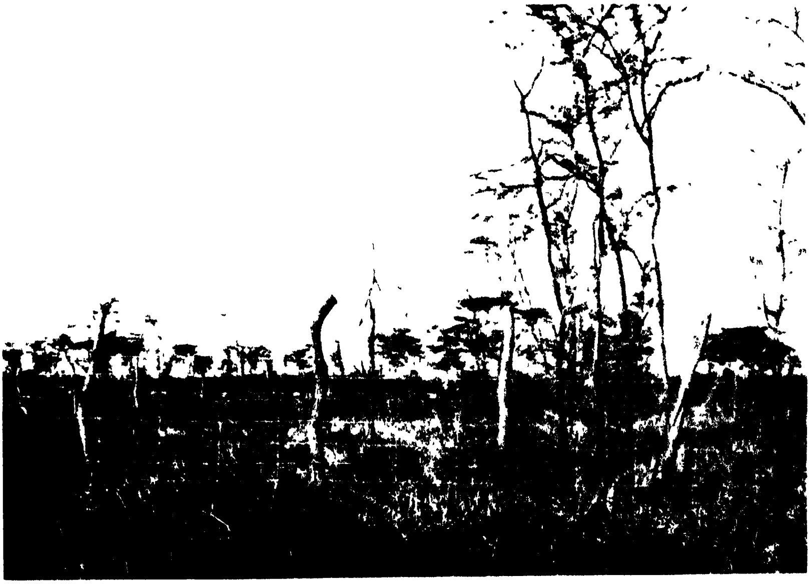


Phot 3. Plot D 2 during the Dry Season after the fires Stevenson screens and various instruments visible. *Acacia formicarum* and one *A. usambarensis*.

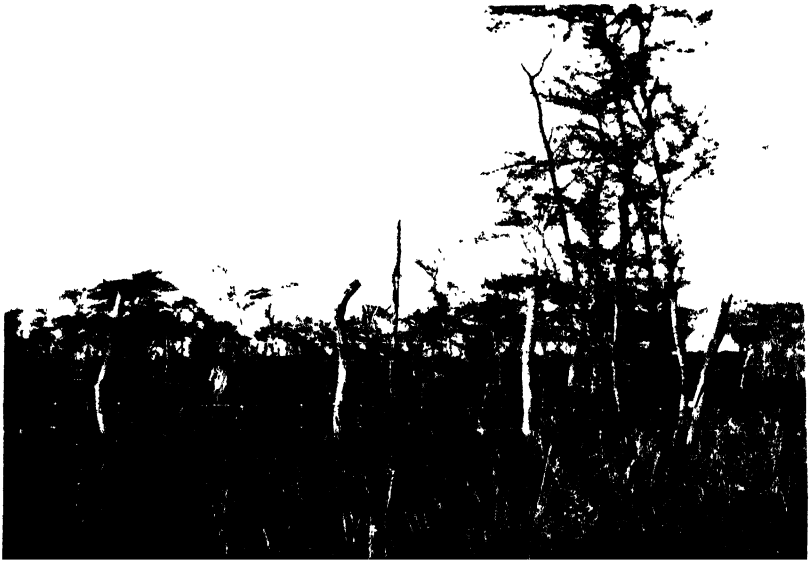


Phot. 4. Thickening up of vegetation in *Acacia formicarum* community after 2 years' protection from fire.

SCOTT—TANGANYIKA COMMUNITIES



Phot. 5 Plot D 1 after 1 year's protection from fire Young regeneration of *Acacia formicarum* visible.



Phot. 6. Plot D 1 after 2 years' protection. Much young *Acacia formicarum* and *Dichrostachys*.

SCOTT—TANGANYIKA COMMUNITIES

Face p. 203

atmometer at 48 in. There is not much difference between evaporation from the white bulbs at 6 and 48 in. during the dry season but the difference increases with the growth of the ground cover.

Mean monthly evaporation in c.c. per hour from the four atmometers in October and April is as follows (see Fig. 7, p. 216):

	Black (48 in.)	White (48 in.)	Black (6 in.)	White (6 in.)
Oct. 1929	2·87	2·29	3·17	2·21
April, 1930	0·67	0·35	0·24	0·16

Although there was very little overhead canopy and although the distance from the standard gauge was only 400–500 yards, the rainfall measured in a gauge at 4 ft. from the ground in this community was 46·58 in. in 1929–30 (6·91 in. less than *B* 2) and 29·06 in. in 1930–1 (4·64 in. less than in *B* 2).

Vegetational features.

Consocies of *Acacia formicarum* and associes of *Ac. formicarum*, *Ac. Seyal* Del. and *Ac. Seyal* var. *fistula* Oliv. are found at Kikori. The experimental plots were laid out in the *Acacia formicarum* consocies. *Dichrostachys glomerata* and occasional *Acacia usambarensis* and *Albizzia hypoleuca* are also found within this community. The canopy is very light, the trees are fairly widely spaced, are small and have very little crown.

Most numerous amongst the ground flora are *Anthephora* sp., *Digitaria* sp., *Panicum maximum*, *Themeda triandra*, *Acalypha* sp., *Aspilia* sp., *Commelina* sp. and *Hibiscus cannabinus*. Other members of the ground flora are: *Aristida Steudelliana*, *Cynodon dactylon*, *Ischaemum* sp., *Pennisetum massaicum*, *Setaria Holstii*, *S. equatorialis*, *Sorghum versicolor* and *Sporobolus* near *indica*; *Tragia* sp. and *Phyllanthus* sp.; species of *Crotolaria*, *Indigofera*, *Tephrosia*; *Corchorus*, *Cyperus* and *Polygala*; and *Cleome monophylla*.

After the rains the first plants in flower are small Cyperaceae with white flowers. In January *Panicum maximum*, *Pennisetum massaicum*, *Indigofera* sp. and *Cleome monophylla* come into flower. By February, *Themeda triandra*, *Sporobolus* near *indica*, *Digitaria* sp., *Cynodon dactylon* and *Tragia* sp. are in flower and *Cleome* is in fruit. In March *Panicum maximum* begins to set seed and *Digitaria* sp. becomes dominant. *Ischaemum* sp., *Anthephora* sp. and *Aristida Steudelliana* come into flower as well as the herbs—*Crotalaria* spp., *Aspilia* sp. and *Hibiscus cannabinus*, the last-named being very numerous.

By the end of April most of the herbs and grasses are in seed although *Sorghum versicolor* may still be in flower. From this time on, the vegetation gradually dries up.

The leaves of *Acacia formicarum* and *Ac. Seyal* are usually shed in September–October. At the end of September, the trees are defoliated and the herbs and grasses are dry and yellow.

E. CONSOCIES OF *ACACIA USAMBARENSIS* (STINKBARK ACACIA).

Soil.

The soil is alluvial clay loam with a total colloid content of 36 per cent. at the surface and 45 per cent. in the subsoil.

The M.W.R.C. at the surface is only 40 per cent. and at 1 ft. is 28–30 per cent. while the hygroscopic coefficients at these depths are 7–9 and 5–8 per cent. respectively. The organic content ranges from 11 per cent. at the surface to 6 per cent. in the subsoil.

There is not much range in the *p*H at different depths although the surface soils are slightly acid (*p*H 6·9) and the subsoil at 1 ft. depth slightly alkaline (*p*H 7·1).

The soil is inundated only for very short periods during the rains, if at all, but is nevertheless quite impermeable at that season. Holards at the surface range from 50 per cent. in the rains to 2 per cent. in the dry season, and from 23 per cent. in the rains to 4 per cent. in the dry season at 1 ft. depth. W.S.P. of the soil at 0–2 in. was 0·14 gm. per hour at a holard of 25 per cent. and 0·002 gm. per hour at a holard of 8 per cent.

During the dry season the soils are very closely packed and are very hard. Very little cracking takes place, the shrinkage varying from 6 per cent. at the surface to 3 per cent. in the subsoil. The soils are still fairly impermeable in the dry season. Big differences in permeability are found when determinations of time taken for 1 litre of water to disappear into 1000 c.c. of soil are made. At 0–10 cm. times vary from 4 to 35 min. and at 10–20 cm. from 34 to 79 min. The porosity at both depths is slightly greater in the dry than in the wet seasons, being 0·4–0·5 in the wet seasons and 0·5–0·6 in the dry seasons.

Surface soil temperatures under canopy seldom exceed 115° F., but temperatures as high as 164° F. have been recorded in a focus spot in the plot. The range in temperature at 1 ft. (monthly means) was 64–75° F. and at 5 ft. was 67–78° F. A unique feature here is that at no time during which soil temperatures were taken were the monthly means at 1 ft. higher than those at 5 ft. The lag of the 1 ft. temperatures behind those of the surface soil was about 6 hours and that of the 5 ft. behind the 1 ft. was 4 days.

Aerial conditions.

The temperature ranges here are not as great as in the more exposed plots, due no doubt to the heavy canopy throwing much shade by day and preventing much radiation by night. The highest absolute maximum temperature recorded was 92° F. and the lowest minimum was 41·75° F. Solar radiation temperatures were rather low compared with those in plots with which we have already dealt. The highest maximum obtained was 143·25° F. Lowest grass minimum temperatures were 41° F. at 48 in. and 43° F. at 6 in. As these were recorded when there was fairly dense ground cover, it is not surprising that the screen minimum recorded a lower temperature (42° F.) than the 6 in. grass minimum thermometer. As in most of the communities already described the grass minimum thermometer recorded lower temperatures than the 48 in. instrument for the period when the ground cover was burned or short.

Relative light intensity at midday in bright sun, but under canopy, varied from 13 to 40 per cent. at 4 ft. from the ground.

For a short period during the dry season, the wind velocities were almost as high as those in the open plot (*B* 2), the maximum over 24 hours being 4·05 m.p.h. During the rainy season (in March), however, when the ground cover was very high and dense, the maximum wind velocity at 48 in. over 24 hours was 0·18 m.p.h.

Here, unlike those plots previously discussed, the evaporation from the black atmometer at 6 in. is always lower than that from the corresponding instrument at 48 in., even after the fires, but for a while it is higher than that from the white atmometer at 48 in. The grass cover becomes so dense during the second rainy season that evaporation from the 6 in. atmometers is cut down to an absolute minimum.

Mean monthly evaporation from the four atmometers in c.c. per hour for October and April are:

	Black (48 in.)	White (48 in.)	Black (6 in.)	White (6 in.)
Oct. 1929	2·47	2·22	2·31	1·95
April, 1930	0·42	0·29	0·12	0·08

Two rain-gauges were placed in this community, one in the plot under canopy and one in an open space about 30 yards away. The loss due to interception by the trees was marked, the rainfall in the gauge in the open being 44·60 in. in 1929–30 and 32·20 in. in 1930–1, while the rainfall recorded by the gauge under canopy was 37·38 in. in 1929–30 and 26·46 in. in 1930–1.

Vegetational features.

Acacia usambarensis forms quite extensive consocies at Kikori. In some parts it is found in an associes with *Ac. campylacantha.* Other trees found in this community are: *Acacia verugera, Allophyllus africana, Bauhinia Thonningii* (*reticulata*), *Combretum splendens, C. Zeyheri, Dichrostachys glomerata* (*nutans*), *Kigelia aethiopica, Lannea humilis, Lonchocarpus* (*Derris*) *violaceus* and *Markhamia lanata* (*Dolichandrone obtusifolia*).

Chief amongst the ground flora we find *Chloris gayana, Digitaria* spp., *Panicum maximum, Commelina* sp., *Acalypha ciliare* and *Hypoestes* sp. Others occurring are: *Chloris paspaloides, Cynodon dactylon, Eragrostis superba, Heteropogon contortus, Hyparrhenia cymbaria, Hyparrhenia Ruprechtii, Sporobolus* sp. and *Themeda triandra*; *Hibiscus dongolensis, Harrisonia abyssinica, Hoslundia opposita* and *Vernonia* sp.

Seedlings of *Commelina* sp. and *Vernonia* sp. are the first to appear after the vegetation has been burned. They are followed by the grasses *Panicum* *maximum*, *Sporobolus* sp. and *Chloris gayana*. *Panicum* and *Sporobolus* reach a height of 2 m. when flowering in February. *Acalypha ciliare* comes into flower at this time too, but *Panicum maximum* is the dominant member of the ground flora. In March *Panicum maximum* and *Sporobolus* sp. are in seed, while *Chloris gayana* is the dominant grass for a while. *Vernonia* sp., *Hypoestes* sp., *Hoslundia opposita* and *Commelina* sp. are found in flower and *Acalypha* is in seed. By May most of the grasses are in seed or have finished seeding, *Hypoestes* and *Hoslundia* are still in flower and *Acalypha* in seed. In July all the plants are yellow or wilting, though *Vernonia* sp. may still be flowering. In September *Acacia usambarensis* and most of the other trees are defoliated and the ground flora is dry and yellow.

F. ECOTONE OF *ACACIA USAMBARENSIS*-*BERLINIA*-*COMBRETUM*-OTHER SPP.

Although the experimental plots are some distance from any *Berlinia globiflora* Harms or associated trees, and although they are in an area containing mostly *Acacia usambarensis* and *Combretum* spp., it was thought best to demarcate a fairly large piece of vegetation containing a large number of different tree species, as the *Acacia usambarensis*-*Berlinia*-*Combretum*-Other spp. ecotone.

Soils.

As might be expected, there is a considerable difference in the soils in different parts of this ecotonal region, which stretches from eluvial soils on one side to alluvial soils on the other. The actual experimental plots were placed on alluvial soil with a total colloid content ranging from 37 per cent. at the surface to 44 per cent. in the subsoil.

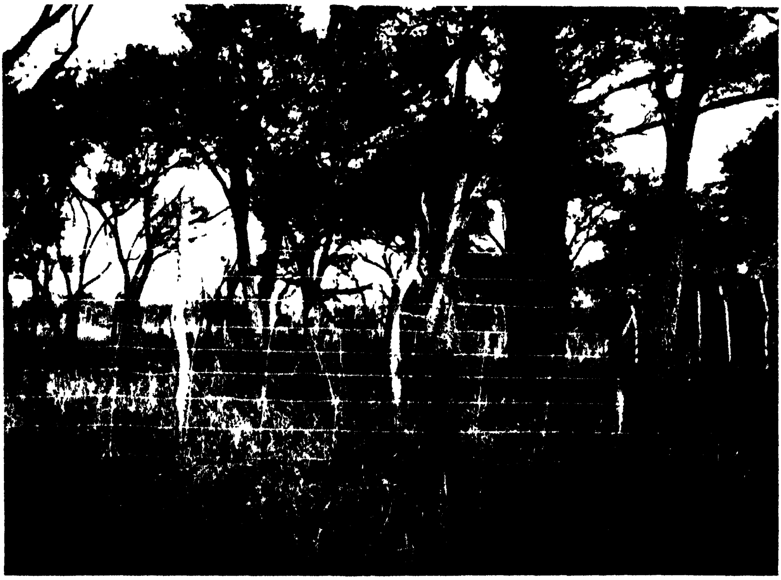
The M.W.R.C. is 35–40 per cent. at the surface and ranges from 25 to 40 per cent. at a depth of 1 ft. At the corresponding depths, the hygroscopic coefficients are from 4 to 7 per cent. and from 3 to 7 per cent. respectively.

The organic content is low, ranging from 4 to 7 per cent. at the surface and from 3 to 6 per cent. in the subsoil.

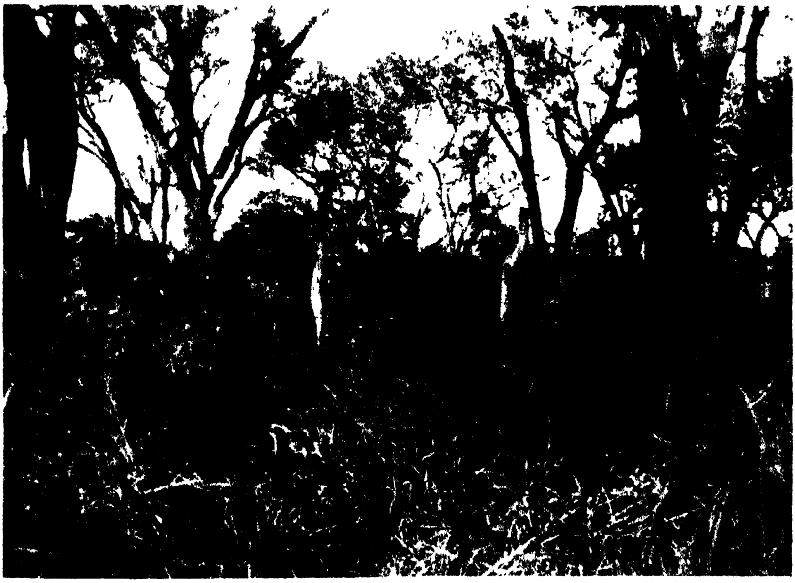
The maximum holards in the rains are about 28 per cent. at the surface and 26 per cent. at a depth of 1 ft. During the dry season holards as low as 1 per cent. at the surface and 4 per cent. in the subsoil may be obtained.

The permeability of the soils in the dry season shows wide ranges in quite small areas, a litre of water taking from 8 to 40 min. to disappear into 1000 c.c. of soil at 0–10 cm., and from 5 to 19 min. at 10–20 cm. depth.

It is rather strange that the soils at 10–20 cm. depth should be much more permeable than those at 0–10 cm. here, for in all the other soils which we have described the permeability at the surface has always been the greater. Rather anomalous results are obtained in porosity determinations too, some



Phot. 7. Plot E 1 in the Dry Season, 1929. *Acacia usambarensis* present, with *Combretum splendens* on the extreme right.



Phot. 8. Plot E 1 after 2 years' protection from fire. Note the thick growth of *Harrisonia abyssinica*.

of the soils having a higher porosity in the rains than in the dry season. The range, however, is very small, being for the most part between 0·4 and 0·5.

Surface soil temperatures are rather higher than those recorded under canopy in Station *E*, a maximum of 135° F. being obtained in the dry season. Soil temperatures (monthly means) at 1 ft. range from 68 to 86° F. and those at 5 ft. from 71 to 84° F. The temperatures at 5 ft. are greater than those at 1 ft. for all except about 3 months in the year. The lag of the temperatures at 1 ft. is 10 hours behind that of the surface soil, and the temperatures at 5 ft. lag about 6 days behind those at 1 ft.

Aerial conditions.

The overhead canopy in this area is not as thick as that in the *Acacia usambarensis* consocies, the relative light intensity ranging from 20 to 40 per cent. As a result the temperature range here is wider than in *E*. The highest absolute maximum temperature obtained was 92·75° F. and the lowest minimum was 40·0° F.

The lowest temperatures recorded by the grass minimum thermometer at 48 in. was 39·25° F. and at 6 in. 41·75° F. Here too we find the screen minimum temperature lower than that of the 6 in. grass minimum thermometer during the coldest month of the year (July) owing to the fact that the grass cover is still unburned. The grass minimum temperatures at 6 in. are lower than those at 48 in. for a short period after the grass has been burned.

The highest wind velocity over 24 hours was 2·44 m.p.h. and during the second rainy season (in March) the mean velocity per hour over the month was only 0·04 mile, with a maximum during that month of 0·14 m.p.h.

The highest mean monthly sunshine was 5·2 hours per day at a time when the canopy was reduced to a minimum owing to the defoliation of the trees. The lowest mean monthly sunshine recorded was 1·7 hours per day during the second rainy season when the trees were in full leaf. A comparison of these hours of sunshine with those for the open station *B*, makes it possible to obtain some idea of the effect of the overhead canopy.

Evaporation from the black atmometer at 6 in. was never higher than that from the corresponding instrument at 48 in., although very nearly approximating it in the dry season after the fires. For the rest, the evaporation from the black and white bulbs at the two levels followed the general trend outlined for all the other plots already described.

The mean monthly evaporation in c.c. per hour for the months of October and April was:

	Black (48 in.)	White (48 in.)	Black (6 in.)	White (6 in.)
Oct. 1929	3·26	2·29	3·14	2·22
April, 1930	0·64	0·39	0·34	0·17

The rainfall recorded by a gauge at 48 in. under light canopy was 51·14 in. in 1929–30, and 33·05 in. in 1930–1.

Vegetational features.

Fairly extensive associes are formed by *Acacia usambarensis, Combretum Zeyheri* and *C. splendens*, and by *Berlinia globiflora* Harms, *Combretum Zeyheri, C. splendens* and *Terminalia sericea*. The experimental plots were laid out in the first named associes.

Other trees found in this community are *Acacia hebecladoides, Ac. Senegal, Albizzia hypoleuca, A. versicolor, Bauhinia Thonningii, Cassia goratensis, Commiphora Fischeri, C. pilosa, C. Schimperi, Dalbergia* sp., *Dombeya reticulata, Kigelia aethiopica, Lannea humilis, L. Schimperi, Lonchocarpus violaceus, Markhamia lanata, Randia Thunbergii, Thespesia* sp., *Turraea Randii* and *Ximenia americana.*

The ground flora in this community is also very large. It would be difficult to point out any marked seasonal aspects other than that the first in flower are the grasses which, for some time, are more numerous and more conspicuous than the herbs. By March, however, most of the grasses have set or shed seed and the herbs become much more noticeable and continue flowering after all the grasses have shed their seed and have begun to turn yellow.

Among the grasses we find *Anthephora* sp., *Brachiaria dictyoneura, Cynodon dactylon, Digitaria* spp., *Eragrostis aspera, E. superba, E. tenuifolia, Heteropogon contortus, Hyparrhenia rufa, H. Ruprechtii, Panicum maximum, P. spicatum, Pennisetum ciliare, Setaria aurea, S. rubiginosa, Sporobolus* sp. (very tall with very small flowers) and *Themeda triandra.*

Among the herbs there are *Cassia* sp. (small, yellow flowered herb), *Crotalaria* sp., *Gloriosa superba* and *Indigofera* sp.; *Acalypha ciliaris, A. sinensis, Euphorbia* sp. and *Tragia* sp.; species of *Oldenlandia* and *Pentanisia*; also *Emelia* sp. and *Vernonia* sp.; *Cissus* sp., *Commelina* sp., *Hypoestes* sp., *Lantana* sp., *Hoslundia opposita, Hibiscus dongolensis* and *H. cannabinus* (rare).

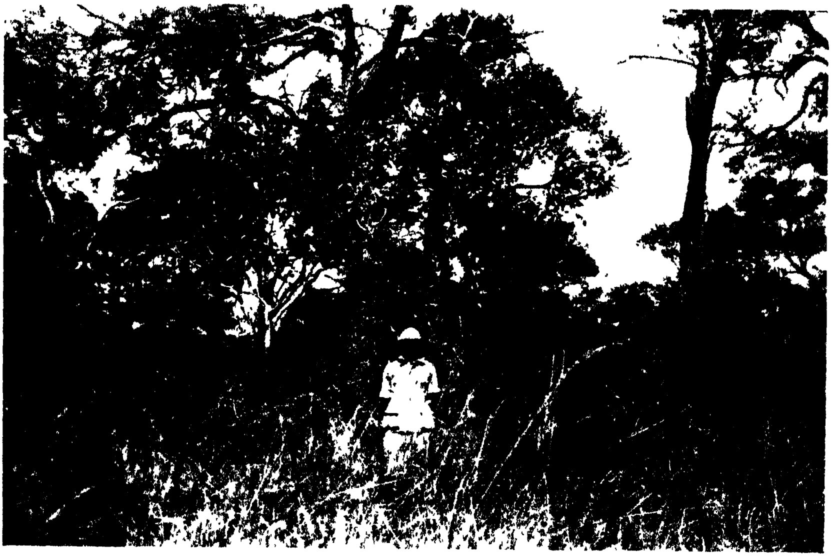
It is not surprising that there should be such a large ground flora, with so many species found on both eluvial and alluvial soils, when it is remembered that this is an ecotone.

G. *COMBRETUM*-OTHER SPP. OPEN WOODLAND.

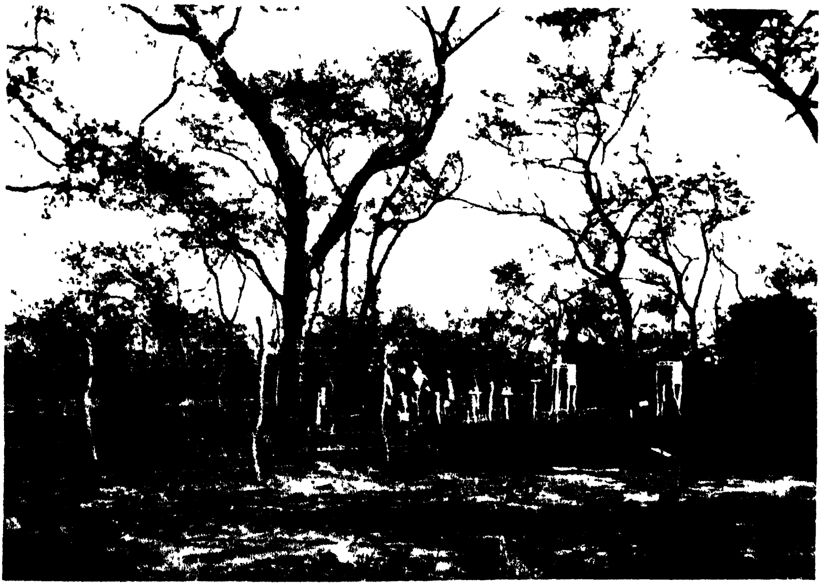
Soils.

The soils are alluvial and have a total colloid content of 30–40 per cent. at the surface and 47–57 per cent. at 1 ft. depth. They vary somewhat in profile, some having a black clay subsoil and others having a yellow clay subsoil. The yellow subsoil has a higher colloid content than the black and its surface soil has a higher colloid content than that above the black subsoil.

The M.W.R.C. at the surface varies from 28 to 30 per cent. and at 1 ft. from 30 to 35 per cent. The hygroscopic coefficient at the surface is 5–6 per cent. and at 1 ft. is 12–17 per cent. These soils are peculiar, compared with those described earlier, in having a higher M.W.R.C. in the subsoil than at the surface,



Phot. 9. Thicket of *Dichrostachys glomerata* after 2 years' protection from fire.



Phot. 10. Plot F 2 during the Dry Season, *Combretum Zeyheri* in the left background, and *Acacia usambarensis.*

SCOTT—TANGANYIKA COMMUNITIES

and in there being such a vast difference between the hygroscopic coefficients at the two depths. The organic content is 5–6 per cent. at the surface and 4–5 per cent. below. There is very little range in *p*H with increase in depth of soils. The surface soils have a *p*H of 7·49 and the subsoils of 7·55.

There is practically no cracking during the dry season, the shrinkage ranging from 0·3 to 4·3 per cent. Instead, a very hard "cement" is formed.

The maximum holards at the surface in the rains were 36 per cent. and at 1 ft. depth were 32 per cent. Minimum holards were found to be 0·6–1 per cent. at the surface and 5 per cent. in the subsoils. The W.S.P. was 0·20 gm. per hour when the holard was 18 per cent., but during the dry season when the holard was about 1 per cent. the W.S.P. was less than 0·001 gm. per hour. With a holard of 2–3 per cent. the W.S.P. was found to be 0·006 gm. per hour.

The soils are not very permeable either in the dry or rainy seasons. During the dry season 1 litre of water takes 45–60 min. to disappear into 1000 c.c. soil at 0–10 cm. depth, and 47–112 min. in the wet season. At 10–20 cm. the time taken in the dry season is 27–32 min. but, in the rains, it is 2 hours in some parts while in others there is standing water at a depth of 10–20 cm. A peculiar feature here is that the permeability of the subsoil in the dry season is greater than that of the surface soil. The porosity of these soils in the wet season is greater than in the dry season, a very different state of affairs from that which exists in all other soils with which we have dealt. It may be due to the "cement" formation when the soils dry. In the dry season the porosity at both surface and subsoil is 0·44–0·45, but in the rains, it varies from 0·54 to 0·62 at the surface and from 0·48 to 0·51 in the subsoil.

Surface soil temperatures are not very high during the year. The highest on record is 124° F. Temperatures (monthly means) at 1 ft. range from 70 to 87° F. and 5 ft. temperatures from 71 to 82° F. The temperatures at the greater depth are highest from February to August. The lag of the temperatures at 1 ft. behind those of the surface soil is 4–6 hours, and of the 5 ft. temperatures behind those at 1 ft. is 3–4 days.

Aerial conditions.

Temperature conditions within this vegetation are fairly extreme. The highest absolute maximum recorded was 96·5° F. and the lowest minimum was 39·5° F. Solar radiation temperatures—absolute maximum per month—were seldom below 150° F. and the mean monthly maxima were always above 135° F. Lowest temperatures recorded by the grass minimum thermometers were 37·75° F. at 48 in. and 39·50° F. at 6 in. For about 2 months in the year—just after the annual fires—the temperatures were lower at 6 than at 48 in.

The highest sunshine per day (monthly mean) under the canopy of *Combretum Zeyheri* was 7·1 hours per day at the end of the dry season, and the lowest monthly mean was 1·7 hours per day during the second rainy season when the trees were in full leaf. Relative light intensity at 48 in. on bright sunny days at midday was 100 per cent. in the open, and under canopy ranged from 15 to 50 per cent. Relative light intensity under thicket was from 0·3 to 1·7 per cent. at midday.

The wind velocities recorded were very low. The highest maximum per day was 3·89 m.p.h. The highest monthly mean was 3·00 m.p.h. and the lowest was 0·30 m.p.h.

Evaporation from the black atmometer at 6 in. was always lower than from that at 48 in., but higher than that from the white atmometer at 48 in. for 4–6 months in the year.

Mean monthly evaporation from the four atmometers in c.c. per hour for October and April were:

	Black (48 in.)	White (48 in.)	Black (6 in.)	White (6 in.)
Oct. 1929	3·14	2·44	—	2·42
April, 1930	0·77	0·42	0·54	0·25

The rainfall recorded in this plot was 47·74 in. in 1929–30 and 32·00 in. in 1930–1. The gauge was in the open. Another gauge was placed in one of the numerous clumps of thicket scattered about in this community, in order to get some idea of the rainfall interception by the thicket. In 1929–30 this gauge, which was less than 50 yards from that in the plot, recorded only 32·69 in. rain and only 28·42 in. in 1930–1.

Vegetational features.

This community at Kikori is characterised by a very open stand of small trees (3–10 m. in height), forked low and having small crowns. Here and there are found small patches of thicket which are prevented from spreading only by the ever-recurring grass fires.

The principal species forming consocies or associes at Kikori are *Combretum Zeyheri*, *C. splendens*, *Acacia hebecladoides*, *Lannea humilis*, *Commiphora Fischeri* and *Terminalia sericea*. Other species found in this community are: *Acacia spirocarpa*, *Bauhinia Thonningii*, *Cassia goratensis*, *Commiphora pilosa*, *C. Schimperi*, *Gardenia Thunbergia*, *Randia Thunbergii*, *Tamarindus indica* and *Thespesia* sp.

The chief thicket-forming species are *Harrisonia abyssinica*, *Grewia bicolor*, *G. fallax*, *G. pachycalyx*, *Allophyllus africanus*, *Rhus* spp., *Euclea multiflora* and *Zizyphus mucronata.*

The grasses are mainly *Cymbopogon excavatus*, *Digitaria* spp., *Heteropogon contortus*, *Hyparrhenia rufa* and *Setaria aurea*. Others occurring are *Aristida Steudelliana*, *Andropogon* sp., *Brachiaria dictyoneura*, *Eragrostis ciliata*, *Microchloa indica*, *Panicum maximum*, *Pennisetum massaicum*, *Setaria rubiginosa* and *Sporobolus indica.*

Among the herbs we find *Blepharis acanthoides*, *Chlorophytum* sp., *Corchorus* sp., *Cyperus* sp., *Ipomaea* sp., *Oldenlandia* sp., *Ocimum* sp., *Phyllanthus* sp., *Polygala* sp., *Rhamphicarpa montana* and *Striga* sp. (parasitic on the grasses).

Soon after the first rains, before the grasses have grown much, the veld is covered by a blaze of colour due to the pink flowers of *Rhamphicarpa montana* and the white flowers of species of *Chlorophytum* and Cyperaceae. Among the first grasses to come into flower are *Microchloa indica, Panicum maximum, Eragrostis* spp. and *Setaria aurea.* By February *Setaria aurea* is the dominant grass and *Themeda triandra, Cymbopogon excavatus, Heteropogon contortus* and *Hyparrhenia rufa* have come into flower, as well as species of *Ipomaea* and *Phyllanthus,* and *Gladiolus quartinianus.* In March the earlier flowering grasses set seed and *Hyparrhenia rufa* becomes the dominant grass. In April most of the grasses are in seed and *Striga* sp. comes into flower. From May onwards the plants begin to dry, and by the time that the trees are defoliated in August–September the grasses and herbs are dry enough to burn.

H. *BERLINIA* WOODLAND—("MIOMBO").

Soils.

The soils are eluvial and sandy with a colloid content of 12–20 per cent. at the surface and 18–22 at 1 ft. depth.

The M.W.R.C. is as high as 45 per cent. at the surface and 28 per cent. in the subsoil, but the hygroscopic coefficient is only 3 per cent. at the surface and 2·5–3 per cent. in the subsoil.

The organic content ranges from 4 per cent. at the surface to 2 per cent. below. The *p*H at the surface is 7·60 and decreases to 6·98 at a depth of 1 ft. Shrinkage is negligible and there is no cracking when the soils are dry.

The highest holards obtained during the rainy seasons were 22 per cent. in the surface soil and 15 per cent. in the subsoil, while in the dry season the lowest holards recorded for these depths were 0·2–0·4 and 3 per cent. respectively. The W.S.P. of the soils is low, being 0·0001–0·001 gm. per hour in the dry season, and reaching a maximum of 0·19 gm. per hour in the rainy seasons.

There is not much difference in permeability at different seasons. The time taken for a litre of water to disappear into 1000 c.c. of soil at 0–10 cm. was 4–6 min. and at 10–20 cm. was 6–11 min. The porosity did not vary much from season to season either. In some cases it was higher in the wet than in the dry seasons while in others the reverse was found. Porosity ranged from 0·42 to 0·46 at the surface and from 0·44 to 0·51 in the subsoil.

Surface soil temperatures seldom reached 89° F. under heavy canopy but, in exposed sites, temperatures as high as 125° F. were recorded. The range of mean monthly temperatures at 1 ft. was 66–80° F. and at a depth of 5 ft. was 68–76° F. Except for about 3 months in the year, the soil temperatures at 5 ft. were greater than those at 1 ft. The lag of the 1 ft. temperatures was 6–8 hours behind those of the surface soil and soil temperatures at 5 ft. were 2–3 days behind those at 1 ft.

Aerial conditions.

The ranges in temperature in this vegetation are lower even than those in the *Acacia usambarensis* consocies. The highest absolute maximum recorded here was 92·0° F. and the lowest minimum was 44° F. The highest absolute maximum solar radiation temperature was 157·0° F. but the mean monthly maxima seldom exceeded 135·0° F., and as low a monthly mean as 100·0° F. was recorded during the rainy season in May, 1930. The lowest grass minimum temperatures at 48 and 6 in. were 44 and 45° F. respectively.

The wind was cut off by the trees to a great extent. The highest velocity recorded over 24 hours was 2·6 m.p.h. and, in April, 1930, the mean velocity for the month was only 0·25 m.p.h.

The highest mean sunshine for any day in the year was 8·4 hours when the trees were defoliated. During the rainy season, when the trees were in full foliage, it dropped to 0·6 hours per day. Photometric measurements by means of the Eder-Hecht "Graukeil" photometer (see Phillips, Scott and Moggridge, 1930) ranged from 0·019 (monthly mean) Bunsen-Roscoe units per second when the trees were defoliated, to a monthly mean of 0·004 Bunsen-Roscoe units per second when the trees were in full foliage. Relative light intensity, measured by means of a Clements stopwatch photometer, ranged from 10 per cent. under full canopy in the wet seasons to 40 per cent. when the trees were defoliated.

Evaporation from the black atmometer at 6 in. was higher than that from the corresponding instrument at 48 in. for about a month in the year, but it was greater than that from the white atmometer at 48 in. for the greater part of the year. This was due, no doubt, to the fact that the ground cover was relatively sparse. For the same reason there was not much difference in evaporation from the white bulbs at 48 and 6 in. throughout the year.

Mean monthly evaporation in c.c. per hour from the four atmometers for October, 1929, and April, 1930, was:

	Black (48 in.)	White (48 in.)	Black (6 in.)	White (6 in.)
Oct. 1929	2·38	1·99	2·94	1·98
April, 1930	0·49	0·31	0·33	0·20

Despite the fairly heavy canopy, the rainfall recorded by a gauge at 48 in. in this plot was very little less than that recorded by the corresponding gauge in the open at the standard station. This may have been due to either of two factors: viz. (1) the rainfall close to the escarpment may have been greater than that farther away, or (2) in addition to actual rainfall, there may have been a drip from the foliage of the trees. It is a pity that there was no open site close at hand for a control gauge. The rainfall recorded in this plot was 51·59 in. in 1929–30 and 28·43 in. in 1930–1.

Vegetational features.

The principal sub-communities within this community at Kikori are *Berlinia globiflora* Harms consocies and associes of *Berlinia globiflora* and *Brachystegia microphylla* Harms.

Other trees and shrubs found within these sub-communities are: *Albizzia versicolor, Boscia salicifolia, Cissus* spp., *Combretum splendens, C. Zeyheri, Commiphora Fischeri, C. pilosa, C. Schimperi, Dichrostachys nyassana, Erythrina tomentosa, Euphorbia Grantii, Lannea Schimperi, Markhamia lanata, Ochna ovata, Pseudolachnostylis maprounaefolia, Randia Thunbergii, Sclerocarya birrea* var. *multifoliata, Strychnos* spp., *Terminalia sericea* and *T. torulosa.*

Among the grasses present we find species of *Andropogon, Aristida, Digitaria* and *Eragrostis*; also *Brachiaria dictyoneura, Heteropogon contortus, Hyparrhenia rufa, H. Ruprechtii, Microchloa indica, Panicum maximum, Rhynchelytrum roseum* and *Setaria aurea.*

Present also are species of the legumes, *Cassia* (prostrate herb), *Crotalaria, Dolichos* (small yellow-flowered climber), and *Indigofera*; Composites and Cyperaceae; species of *Commelina, Ocimum, Oxalis, Ipomaea, Pentas* and *Striga*; *Acalypha ornata, A. sinensis, Rhamphicarpa montana, Temnocalyx obovatus* and *Tephrosia incaria.*

Species of *Commelina* are the first in flower after the rains. These are followed by the grasses *Microchloa indica, Eragrostis* spp., *Digitaria* spp. and *Brachiaria dictyoneura*, all of which, with the exception of *Microchloa indica*, reach a height of 120 cm. By February *Panicum maximum, Rhynchelytrum roseum, Temnocalyx obovatus, Oxalis* sp., *Cassia* sp. and *Striga* sp. are in flower. First *Digitaria* sp. is dominant but it gives way to *Panicum maximum* which, in its turn, makes way for *Hyparrhenia rufa.* By April all the grasses except *Hyparrhenia rufa* have shed their seed and are beginning to turn yellow. In July all the grasses and herbs have shed their seeds and are almost dry.

K. UPLAND CONSOCIES OF *BRACHYSTEGIA MICROPHYLLA.*

Soils.

These are very shallow eluvial soils with much exposed rock bare of any soil. As a result, determinations of physical factors could be made only at the surface, for the rock was always within 1 ft. of the top of the soil.

The colloid content of the soil was 24 per cent., the M.W.R.C. over 100 per cent. The hygroscopic coefficient was 14 per cent. and the organic content 18 per cent. The porosity varied from 0·6 to 0·7.

Holards varied from 80 per cent. in the rains to 1 per cent. in the dry season. W.S.P. of the soil ranged from 0·0004 gm. per hour at a holard of 1 per cent. to 0·20 gm. per hour at a holard of 54 per cent.

Surface soil temperatures seldom exceeded 100° F.

Aerial conditions.

The maximum temperature registered in this plot was 92° F. and the minimum was 46° F. The highest temperature recorded by the maximum solar radiation thermometer was 151° F. while the monthly means ranged from 106 to 146° F. There was very little difference between temperatures recorded by the grass minimum thermometers at 6 and 48 in. The lowest minimum was 45·75° F. at the lower level.

Relative light intensity under canopy ranged from 18 to 43 per cent. according to the season and hence to the canopy.

The evaporation from the black atmometer at 6 in. was higher than that from the corresponding bulb at 48 in. for only 1 month in the year, but it was greater than that from the white atmometer at 48 in. throughout the year. The white atmometer recorded the lowest evaporation all the year round.

The mean monthly evaporation from the four atmometers in c.c. per hour for April, 1930, and September, 1930, were:

	Black (48 in.)	White (48 in.)	Black (6 in.)	White (6 in.)
April, 1930	0·58	0·39	0·48	0·32
Sept. 1930	1·41	1·30	1·46	1·15

The rain-gauge was installed too late in the rainy season 1929–30 to obtain any useful results for that season. In 1930–1 the rainfall recorded under canopy of *Brachystegia microphylla* was 31·66 in.

Vegetational features.

At Kikori we find *Brachystegia microphylla* in an associes with *Berlinia globiflora* and seldom in a consocies near the plots. Other trees and shrubs occurring are *Albizzia versicolor*, *Cissus* sp., *Commiphora Fischeri*, *Dalbergia* spp., *Lannea Schimperi*, *Parinarium curatellaefolium* and *Vangueria* sp.

Chief amongst the ground flora are *Harpachne Schimperi*, *Digitaria horizontalis*, *Rhynceletrum roseum* and species of *Commelina*, *Emelia*, *Pellaea*, *Bidens* and *Vernonia*. These plants, however, are fairly widely scattered and there is no thick ground cover such as is found in the other vegetation communities.

Rhynchelytrum roseum and *Pellaea* sp. are the first plants seen after the break of the rains. The former soon sheds its seed, but is seen flowering for the second time in April. Most of the herbs—*Commelina* sp., *Bidens* sp., *Emelia* sp. and *Vernonia* sp.—flower in March–April, shed their seed in May, and by June all the plants have shed their seeds and are nearly dry.

EFFECTS OF PROTECTION FROM FIRE.

By means of protecting areas from fire within each community it was hoped to gain some idea of the development of the plant successions, with their subsequent reactions on the soils and aerial conditions. But as observations were taken for less than two years, it was not possible to get more than a mere impression of the general trend of successional development, and the period was far too short for much change to take place in the soil and other factors of the habitat. Such results as were obtained from the study of the soils and aerial conditions will be dealt with first, and then observations on the vegetation, community by community, will be discussed.

SOILS.

It could not be expected that there would be any change in such edaphic factors as total colloid content, M.W.R.C., hygroscopic coefficient, and percentage shrinkage over such a short period; nor was there any noticeable difference between most of the factors which varied from season to season, in the exposed and protected plots. The only factors which were affected at all were: (1) organic content, (2) total water content or holard, (3) W.S.P. of the soils, and (4) soil temperatures.

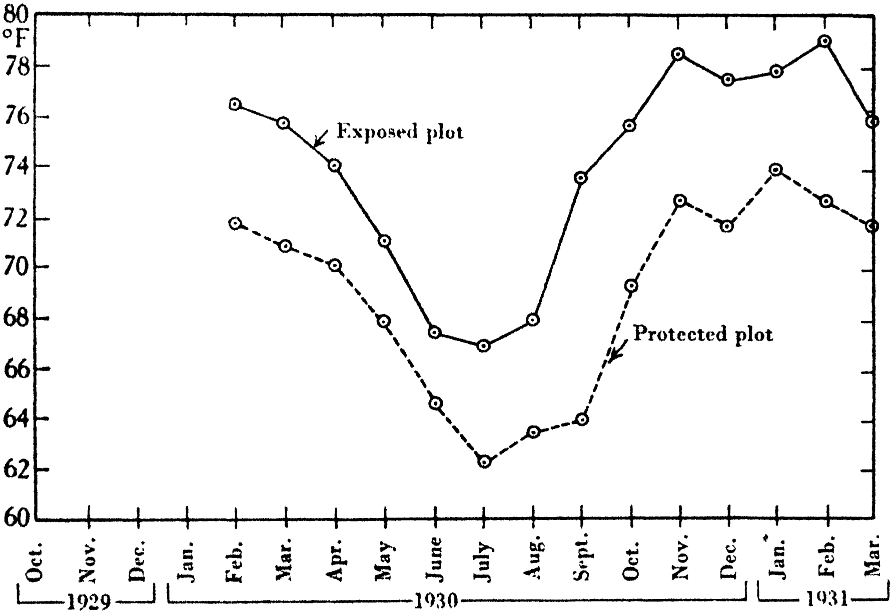


FIG. 6. Contrast of soil temperatures at one foot in exposed and protected plots.

(1) There was a slight increase in organic matter (½–2 per cent.) in most of the soils where the vegetation was protected from fire.

(2) Determinations of the W.S.P. of the soils, taken at weekly intervals over a period of 3 months just before the observations were discontinued (the period being part of the first rains, the short dry season and part of the second rainy season), showed a higher W.S.P. in the soils where the vegetation was protected from fire than where it was exposed to fire.

(3) There was not much difference between the holards in the protected and non-protected areas during the rainy seasons. As a general rule, however,

the holard was greater in the protected areas after the fires had swept through the others, and in the early part of the rains. This is to be expected, since a covering of dry grass would cut down evaporation and would conserve soil moisture, while there would be a good deal of evaporation from a soil surface where the vegetation cover had been burned.

(4) Soil temperatures both at the surface and at 1 ft. depth are lower in the protected than in the non-protected areas throughout the year (see Fig. 6). The difference is not great during the rainy seasons, but in the late dry season it is very marked.

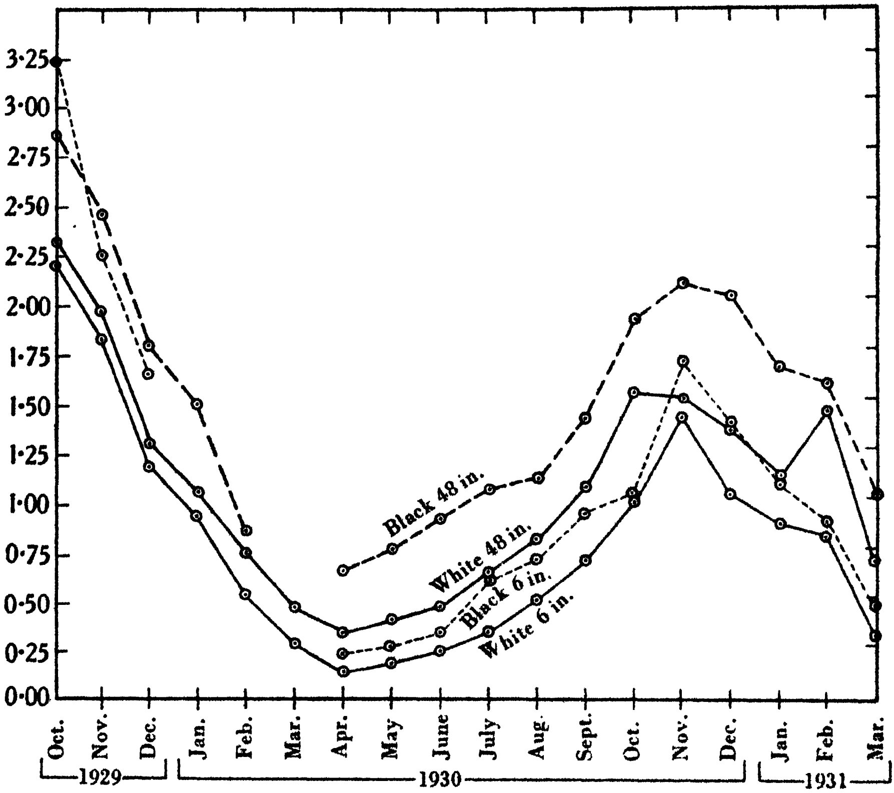


FIG. 7. Evaporation (in c.c. per hour) from black and white atmometers at 48 and 6 in.

AERIAL CONDITIONS.

Owing to a shortage of instruments, it was not possible to instal more than a very few instruments in these protected (No. 1) plots to measure aerial conditions for comparison with results obtained in the non-protected (No. 2) plots.

Three factors in each of the plots can be compared. These are: (1) evaporation from white atmometers at 6 in., (2) grass minimum temperatures at 6 in., and (3) relative light intensity at 6 in.

(1) The evaporation in the No. 1 plots was lower than that in the No. 2 plots throughout the year. There was not very much difference during the rainy seasons but during the long dry season the difference was very marked (see Fig. 8).

(2) The grass minimum temperatures in the No. 1 plots are lower throughout the year than in the No. 2 plots, except for about a month after the fires when the soil is bare. This is rather remarkable as one would have thought that the thick matted vegetation in the protected plots, though not so tall as that in the burned plots during the rainy seasons, would have had a "blanket" effect, cutting off the radiation at night. If such an effect had been realised the grass minimum temperatures in the protected plot would be greater than in the other plot. As this is not so, the height of the vegetation above the soil must have had some effect. The tall grasses in the burned plots might have the greater "blanket" effect during most of the year, and hence the temperatures registered by the grass minimum thermometers would always be higher except when the vegetation cover has been burned.

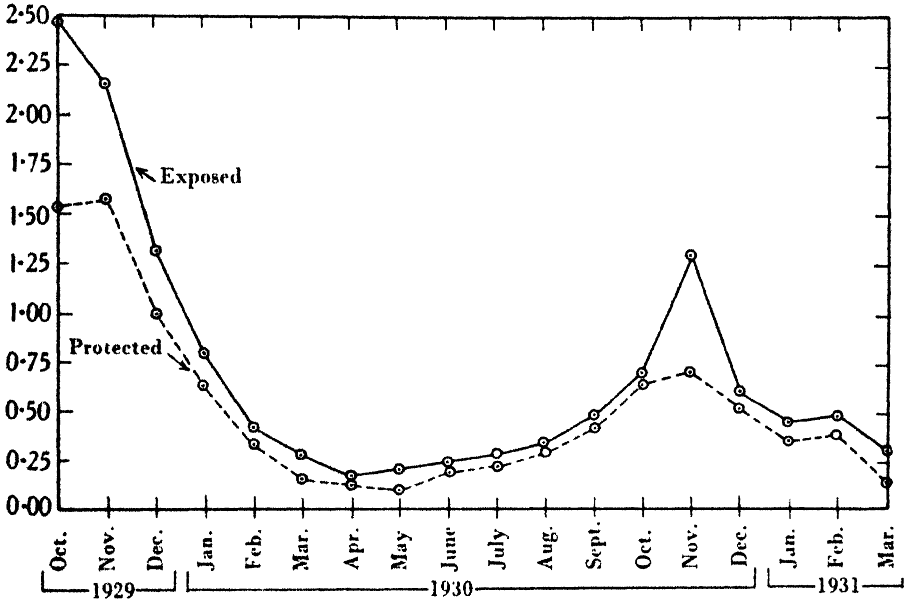


FIG. 8. Evaporation (in c.c. per hour) from white atmometer at 6 in. in exposed and protected plots.

(3) In December, 1930, when the grasses, in the plots which had been burned, had attained heights ranging from 50 to 100 cm., relative light intensity readings were taken in the middle of bright sunny days, at 6 in. above the ground, under the herb-grass cover, in all the No. 1 and No. 2 plots.

In every case the relative light intensity was lower in the No. 1 plot. The proportions of full light intensity in different plots were as follows:

In "Mbuga" plots, *B* 1 and *B* 2 respectively, 1 and 5 per cent.; in the *Acacia formicarum* plots, *D* 1 and *D* 2, 2 and 10 per cent., and in the *Acacia usambarensis* ecotone plots, *F* 1 and *F* 2, 5 and 12 per cent.

VEGETATIONAL FEATURES.

Throughout the various vegetation communities studied it was found that after the beginning of the rainy season the grasses in the burned plots began to shoot up almost immediately, whereas the old dry grasses began to put forth new leaves much later. When the rains broke fairly early and then there was a spell of several weeks with very little rain, the fresh young grasses in the No. 2 plots very soon showed signs of wilting, while the grasses in the No. 1 plots were unaffected.

Quite a number of trees of *Acacia formicarum* were killed by fire in 1930. After a few days of exceptionally early rain in September the trees began to put forth young leaves. Soon afterwards, the fires occurred and the young foliage was so badly scorched that the trees never recovered.

It was found that after two years' protection the number of species of grass was reduced, but the number of perennial herbs, shrubs and trees was on the increase.

A. "*Mbuga*" *Stream-Bed community.*

(Pl. XVIII, Phots. 1, 2.)

After two years' protection from fire, the plot under observation showed a few grasses (*Panicum maximum* and *Digitaria scelaria*), a great deal of *Aspilia* sp. to a height of 300 cm., much *Dolichos* sp., *Cyperus* sp. and a fair number of plants of *Asclepias semilunata* and *Aeschynomene* sp.

The *Dolichos* was gradually smothering all the grasses and annuals, leaving only *Cyperus* sp., the tall *Aeschynomene* sp., *Asclepias semilunata* and *Aspilia* sp.

B. *Seasonal Swamp* ("*Mbuga*") *community.*

Here also the number of species of grass was much reduced, the main species left being *Panicum maximum* and *Ischaemum* sp. The grasses were very much matted by *Dolichos* sp., which was very plentiful. *Asclepias semilunata* and *Aspilia* sp. were on the increase.

It would appear as though the grasses would gradually be ousted or much reduced by *Dolichos* which, in its turn, would make way for the tall, woody, perennial plants.

C. *Ecotone of* "*Mbuga*"-Acacia *spp.*

In the annually burned plot, grasses were very numerous; some *Aspilia* sp. and several annual herbs were present, but there was practically no regeneration of the tree species. A few *Acacia Seyal* coppice shoots were visible but they were burned back every year.

In the protected plot, *Ischaemum* was the most numerous grass while a few others such as *Anthephora* sp. and *Setaria* spp. were very much matted by the *Dolichos*, which was plentiful. *Aspilia* sp. was the most numerous of all the ground flora, but there was a great deal of young coppice of *Acacia Seyal* and *Ac. formicarum* which was growing very fast and forming great thorny clumps. Seedlings of these *Acacia* spp. were also appearing, and one would expect that, within a few years, the whole protected area would be a thick, thorny, impenetrable barrier of Acacias.

D. *Consocies of* Acacia formicarum (*Black Gall Acacia*).

(Pls. XIX, XX, Phots. 3, 4, 5, 6.)

The remaining species of grass in the protected plot at the end of two years were *Digitaria* sp., *Ischaemum* sp., *Panicum maximum* and *Themeda triandra*. These were covered here and there by *Dolichos* sp. and by a great deal of a pink Acanthaceous plant (as yet unidentified). The most noticeable feature here, however, was the rapid development of the young regeneration of *Acacia formicarum* and the thicket-forming *Dichrostachys glomerata* and *Dalbergia melanoxylon*. *Dichrostachys glomerata* was the most numerous, and the development of these species with the *Acacia formicarum* is well illustrated in Pl. XIX, Phot. 4, and Pl. XX, Phot. 6.

E. *Consocies of* Acacia usambarensis (*Stinkbark Acacia*).

(Pls. XXI, XXII, Phots. 7, 8, 9.)

The height of the grasses in the protected plot was very much less than that in the non-protected area during the rainy seasons. The principal grasses were *Chloris gayana*, *Digitaria* sp. and *Panicum maximum*. The number of herbaceous plants—annual and perennial—was on the increase. Chief amongst these were *Hoslundia opposita*, *Hibiscus dongolensis* and *Solanum* sp.

Seedlings of *Acacia usambarensis* and *Harrisonia abyssinica* and coppice shoots of *Harrisonia* were very numerous, growing very fast and forming an incipient thicket (see Pl. XXI, Phot. 8). *Dichrostachys glomerata* (see Pl. XXII, Phot. 9) and *Grewia* spp., where undisturbed by fire, were also forming fast growing clumps of thicket.

F. *Ecotone of* Acacia usambarensis-Berlinia-Combretum-*Other spp.*

(Pl. XXII, Phot. 10.)

The grasses in the protected plot in this community were far more numerous than in any of the protected areas in other vegetation types, but here too the number of annual and perennial herbs and woody plants was tremendously increased. There were large numbers of *Bidens* sp., *Hygrophila* sp., *Vernonia* sp. and *Hoslundia opposita*. Under the *Hoslundia opposita* the grasses were slowly disappearing.

Very large number of seedlings, suckers, and coppice shoots of *Acacia usambarensis*, *Combretum splendens*, *C. Zeyheri*, *Lannea humilis* and *Dichrostachys glomerata* were found developing among the herbs. In several years' time, no doubt, with continuous protection from fire, a fairly thick stand, consisting mainly of *Combretum Zeyheri* and *Dichrostachys glomerata*, would develop.

G. Combretum-*Other spp.* Open Woodland.

There was not much difference in species of grasses in the No. 1 and No. 2 plots after two years of protection of the No. 1 plot from fire. On the whole the grasses were much shorter and more tufted in the No. 1 plot. In the No. 2 plot, however, there was no regeneration of the principal tree species, nor was there much in the way of perennials. In the No. 1 plot, *Hoslundia opposita* was a conspicuous perennial and there were a great many seedlings, suckers and coppice of *Combretum splendens*, *C. Zeyheri*, *Commiphora Schimperi*, *Lannea humilis* and *Harrisonia abyssinica*. Of these, *Commiphora Schimperi*, *Harrisonia abyssinica* and *Lannea humilis* are also constituents of deciduous thicket.

Outside the plots a number of thickets, which were kept in check by the annual fires, were protected for a season, and during this time they developed a good deal in size and density.

H. Berlinia *Woodland* ("*Miombo*").

Here, too, there was no noticeable reduction in species of grass in the No. 1 plot, but the grasses were shorter, more tufted, and thinner on the whole than in the No. 2 plot. The regeneration of tree species was fair.

In the protected plot, very few seedlings, suckers, or coppice shoots could be found, but in the No. 1 plot (one-tenth of an acre in area) there were over 140 seedlings or coppice shoots, from burnt back seedlings, staked and numbered for height increment measurements. Not all the seedlings or coppice in the plot, by any means, were staked. The regeneration consisted chiefly of *Berlinia globiflora*, *Combretum splendens*, *C. Zeyheri*, *Terminalia sericea*, *T. torulosa*, *Dalbergia* sp., *Commiphora Schimperi* and *Randia Thunbergii*.

In a strip of "Miombo" through which a narrow, fairly shallow ravine (10–15 ft. deep) was running, a chart transect 300 ft. long and 10 ft. wide was made at the end of the rainy season in 1930 and re-charted during the rainy season in 1931. The transect was so laid out that it began in the *Berlinia globiflora* consocies, passed through the ravine, on the banks of which thicket was growing, and ended in the *Berlinia* consocies. The object of the transect was to discover whether the thicket on the banks of the ravine would spread, and whether the "Miombo" would give way to *thicket*, i.e. to discover, if possible, whether *thicket* really is climax to *Berlinia* woodland or not.

The experiment was of far too short duration to obtain any positive results. But the decrease in some species and the increase in others, even over this short period, is interesting. There was a well-marked decrease in the numbers of seedlings, suckers and coppice of *Berlinia globiflora*, *Acacia stenocarpa* and *Markhamia lanata*. Very little difference in numbers of *Brachystegia microphylla*, *Combretum Zeyheri*, *Terminalia sericea*, *T. torulosa*, *Allophyllus africana*, *Cassia* sp., *Dalbergia melanoxylon*, *Euclea multiflora*, *Phyllanthus* sp. and *Strychnos* sp. was noted. A definite increase was seen in the numbers of *Commiphora Schimperi*, *Dalbergia* sp., *Dichrostachys* sp., *Harrisonia abyssinica*, *Hoslundia opposita*, *Lannea Schimperi*, *Lonchocarpus* sp., *Pavetta* sp. and *Randia Thunbergii*. Most of these are thicket constituents so it would appear as though the thicket were advancing into the *Berlinia* woodland even within so short a period of protection.

K. *Upland consocies of* Brachystegia microphylla.

There was very little difference between annually burned and protected sites in this community. The only noticeable feature was the appearance of the No. 1 plot of a few seedlings and some coppice of *Brachystegia microphylla* and *Parinarium curatellaefolium* which did not appear in the annually burned plot.

GROWTH INCREMENTS IN HEIGHT AND GIRTH.

In the study of the vegetation at Kikori with an eye to the possible natural thickening up of the vegetation to a type unfavourable to the Tsetse fly, the study of plant successions alone could only indicate whether the successions progressed towards thicker types or not. It was necessary to study the growth increments of the principal tree species within the chief communities in order to discover whether the vegetation would thicken up rapidly enough to be of any use, if protected against fire.

HEIGHT INCREMENTS.

Seedlings and coppice or suckers, formed by the re-shooting of burned back seedlings, were marked by means of wire stakes and numbered. These were measured during the second rainy season and the early part of the dry season 1930, and again in the second rainy season in 1931, so that almost a year elapsed between the two sets of measurements. The following are the results obtained from one year's study of the height increments of seedlings and coppice. The seedlings, suckers and coppice have been divided into different classes according to heights, the classes varying with the species.

As might be expected, the mean increment in height in each species is much greater in the coppice and suckers than in the seedlings. In most of the types under observation, the annual increment increases with the height of the seedling, sucker, or coppice, and the mean annual increments are, on the whole, fairly high.

Table VIII. *Increment in height.*

	Seedlings					Coppice or suckers				
Species	Class in cm.	No.	Dead	Mean increment in cm.	Average mean increment in cm.	Class in cm.	No.	Dead	Mean increment in cm.	Average mean increment in cm.
ANACARDIACEAE										
Lannea humilis	0–20	11	1	3	4	0–20	18	—	6	7
	Over 20	4	—	8		Over 20	11	—	9	
L. Schimperi	No seedlings staked					0–30	10	—	6	8
						Over 30	3	—	14	
BIGNONIACEAE										
Markhamia lanata	No seedlings staked					0–20	9	—	8	13
						20–30	11	—	16	
						Over 30	7	—	16	
BURSERACEAE										
Commiphora Schimperi	0–30	7	1	5	5	0–40	15	3	9	8
COMBRETACEAE										
Combretum splendens	0–20	11	—	5	7	0–50	8	—	8	10
	Over 20	4	—	15		50–80	24	3	13	
						Over 80	14	1	13	
C. Zeyheri	0–10	31	2	4	5	0–20	24	1	7	8
	10–20	50	4	5		20–30	21	1	9	
	Over 20	5	—	6		30–40	13	—	8	
						Over 40	34	—	7	
Terminalia sericea	0–20	8	4	5	5	0–30	18	2	13	20
	Over 20	3	1	6		30–40	21	—	17	
						40–60	22	—	20	
						Over 60	20	—	32	
LEGUMINOSAE										
Acacia formicarum	0–20	12	5	9	11·5	0–30	32	3	12	33·5
	Over 20	4	1	18		30–50	34	5	29	
						50–100	36	1	40	
						Over 100	20	2	29	
A. Seyal	0–30	11	8	12	14	0–30	11	4	7	27
	Over 30	10	7	16		30–100	12	5	12	
						Over 100	15	1	44	
A. usambarensis	0–20	7	2	3	4	0–30	7	2	16	19
	Over 20	5	1	5		30–40	6	—	15	
						Over 40	9	—	23	
Bauhinia Thonningii	No seedlings					0–70	9	2	12	12
						Over 70	8	—	12	
Berlinia globiflora	0–10	154	8	4	7	0–10	29	—	6	11
	10–20	33	2	10		10–20	29	2	8	
	20–30	14	3	17		20–30	16	—	15	
	30–40	3	—	20		30–40	5	—	8	
	Over 40	9	—	22		Over 40	17	4	24	
Brachystegia microphylla	0–10	4	1	4	17	0–20	16	1	4	18
	10–40	—	—	—		20–40	13	1	14	
	Over 40	3	—	35		40–60	11	—	25	
						Over 60	10	—	34	
Dalbergia sp.	0–20	10	—	4	4·5	0–30	19	—	3	7
	Over 20	10	—	5		30–50	10	—	7	
						Over 50	14	—	12	
Dichrostachys nyassana	No seedlings staked					0–30	7	1	8	13
						30–50	6	—	10	
						Over 50	7	—	19	
D. glomerata	0–25	20	11	6	6	0–40	30	12	15	20
						40–60	24	4	18	
						60–80	33	5	20	
						Over 80	26	2	26	
RUBIACEAE										
Randia Thunbergii	No seedlings staked					0–20	8	1	12	18
						20–40	9	—	15	
						Over 40	8	1	29	
SIMARUBACEAE										
Harrisonia abyssinica	No seedlings staked					0–100	20	1	28	67
						100–200	13	—	68	
						Over 200	15	1	109	

GIRTH INCREMENTS.

The results obtained from the study of the girth increments of the principal tree species over a period of one year are given below. The period, for which the increment was taken, was an exceptionally rainy year and hence the increments may be slightly higher or lower than for a normal year.

Table IX. *Increment in girth.*

Species	Class in cm.	No.	Mean increment in cm.	Average mean increment in cm.
ANACARDIACEAE				
Lannea humilis	0–20	15	1·1	1·3
	20–25	9	1·3	
	25–30	12	1·4	
	30–40	8	1·6	
	Over 40	8	1·0	
L. Schimperi	0–30	10	1·1	1·2
	30–40	14	1·3	
	40–50	13	1·3	
	Over 50	14	1·3	
BIGNONIACEAE				
Kigelia aethiopica	0–50	11	0·9	2·0
	50–60	8	1·9	
	60–70	9	2·2	
	70–85	10	2·4	
	Over 85	6	2·6	
Markhamia lanata	0–20	9	1·2	1·7
	20–30	14	0·9	
	30–40	10	2·0	
	Over 40	15	2·4	
BURSERACEAE				
Commiphora Fischeri	0–15	7	1·0	1·4
	15–25	15	1·1	
	25–30	9	1·3	
	30–40	12	1·8	
	Over 40	9	1·7	
Commiphora Schimperi	0–20	10	0·8	1·1
	20–30	7	0·6	
	30–40	5	1·6	
	40–50	8	1·5	
	Over 50	5	1·3	
COMBRETACEAE				
Combretum splendens	0–20	8	1·6	2·2
	20–30	11	1·8	
	30–40	11	1·8	
	40–50	8	2·8	
	Over 50	11	3·1	
Combretum Zeyheri	0–20	8	1·8	2·7
	20–30	16	2·3	
	30–40	13	3·2	
	40–50	7	2·9	
	Over 50	6	3·4	
Terminalia sericea	0–20	8	1·2	1·9
	20–30	10	1·4	
	30–40	11	1·8	
	40–50	9	1·8	
	Over 50	10	3·0	
EUPHORBIACEAE				
Pseudolachnostylis maprounaefolia	0–20	13	0·7	0·8
	20–30	13	0·8	
	30–40	9	1·0	
	Over 40	16	0·8	

Table IX (*contd.*).

Species	Class in cm.	No.	Mean increment in cm.	Average mean increment in cm.
LEGUMINOSAE				
Acacia campylacantha	0–40	8	4·9	6·8
	40–60	6	6·9	
	60–80	9	10·1	
	80–100	6	5·7	
	Over 100	2	3·5	
Acacia formicarum	0–15	7	1·4	1·4
	15–18	10	1·5	
	18–21	15	1·7	
	21–24	9	1·1	
	Over 24	11	1·1	
Acacia nebecladoides	0–20	11	0·8	0·9
	20–30	18	0·6	
	30–40	10	1·2	
	Over 40	12	1·3	
Acacia Seyal	0–40	6	4·1	3·5
	40–50	10	3·3	
	Over 50	11	3·2	
Acacia usambarensis	0–30	8	1·9	1·6
	30–45	10	2·1	
	45–60	8	1·5	
	60–75	15	1·4	
	Over 75	6	1·3	
Acacia verugera	0–50	6	1·6	3·2
	50–60	5	3·0	
	60–70	2	2·8	
	70–80	5	3·7	
	Over 80		4·3	
Bauhinia Thonningii	0–20		1·8	1·0
	20–30		1·1	
	30–40	15	1·0	
	40–50	12	0·8	
	Over 50	12	0·8	
Berlinia globiflora	0–20	4	1·1	1·9
	20–30	6	1·9	
	30–40	18	1·3	
	40–50	14	2·3	
	Over 50	7	2·6	
Brachystegia microphylla	0–30	5	1·4	1·6
	30–40	7	1·0	
	40–50	13	2·0	
	50–60	11	1·4	
	Over 60	14	1·7	
Dalbergia sp.	0–15	12	0·9	1·1
	15–20	13	0·7	
	20–25	11	1·2	
	Over 25	14	1·3	
Dichrostachys nyassana	0–15	19	0·7	0·6
	15–20	20	0·6	
	Over 20	11	0·6	
Lonchocarpus violaceus	0–50	9	2·9	3·2
	50–70	10	2·9	
	Over 70	7	4·0	
RUBIACEAE				
Randia Thunbergii	0–20	19	0·6	0·7
	20–30	15	0·7	
	Over 30	16	0·8	

We find that, with few exceptions, the girth increment either increases with the girth class, or it increases to an optimum and, for girths above this class, the increment gradually decreases. The increments for the three Acacias, viz. *Ac. campylacantha*, *Ac. Seyal* and *Ac. verugera*, are very high. It is of interest to note that these trees are usually found growing close to water and that they are pioneers in the "Mbuga" ecotone.

An interesting phenomenon was noted in the case of *Brachystegia microphylla*. Phillips (1930) states with regard to *Berlinia-Brachystegia* communities: "The community is found upon eluviated sandy loams and clay loams and, while it may be found upon colluvial soils—being rooted in the eluvium below the colluvial cover—it is never found upon alluvial soils.

At Kikori four trees of *Brachystegia microphylla*, growing in apparent alluvial soil near plot *G* (*Combretum* open woodland), were banded for girth increment determinations. There appeared to be no difference between the soil at this spot and the surrounding soil bearing typical *Combretum* open woodland and incipient thicket. The four trees under observation each showed a much greater increment in girth than any other tree of *Brachystegia microphylla* banded for girth increment determinations.

PHENOLOGY.

The periods of defoliation and times of flowering and fruiting of the trees is interesting. Some species (e.g. *Commiphora Fischeri*) would be defoliated some time before the end of the second rainy season. Other species (e.g. *Acacia usambarensis*) would be defoliated for perhaps only a week and fresh leaves would appear before the first rains.

Table X shows the times of appearance and dropping of foliage, and the times of flowering and fruiting of the principal species. Times of flowering, fruiting, etc., would and do, of course, vary from place to place. These are observations for Kikori only. About four species besides those included in the girth and height increment experiments appear in these tables. The letters N.O. stand for "no observations."

CONCLUSIONS.

Although the period during which all these observations were made was far too short to enable anyone to make definite statements with regard to the plant successions and their progress, a careful observer could, by the study of the data collected during the two years 1929–31, draw conclusions as to the *probable* course of the plant successions.

From the study of the soils in the various vegetation communities, one would be inclined to classify the alluvial soils into two main types—the "Mbuga" and the *Combretum* open woodland soils. On examination of the data collected on the properties of these soils, the soils which we might classify

Table X. *Phenology of tree species.*

Family and species	First leaves	Full foliage	Foliage turning yellow	Trees first defoliated	Flower buds	Full flower	Young fruit	Fruit ripe and seed dropped
ANACARDIACEAE								
Lannea humilis	10–11	12	7	8	11	11–12	12	3 on
L. Schimperi	12	12	5–7	8–9	9	9–11	N.O.	N.O.
BIGNONIACEAE								
Kigelia aethiopica	9	12	5	7	N.O.	N.O.	N.O.	N.O.
Markhamia lanata	11–12	12	5–6	7	12	1	2	5–6
BURSERACEAE								
Commiphora Fischeri	11–12	12	4–5	5	11–13	12	3	6 on
C. Schimperi	11	12	6	9	11	11	12	4–6
COMBRETACEAE								
Combretum splendens	9–12	12	5–7	9	9	10–11	12–2	3 on
C. Zeyheri	10–12	10–1	5–8	9	8–12	10–12	2	8–9
Terminalia sericea	10–11	12	5–8	10	12	12–1	1–2	9
T. torulosa	11	12	5–8	9	12	12 1	1–2	5 on
EUPHORBIACEAE								
Pseudolachnostylis maprounaefolia	10–12	11–1	7–9	8–9	11	11	12	4–6
LEGUMINOSAE								
Acacia campylacantha	12	12	8	9	12–1	1–2	2–3	9–10
A. formicarum	10	11–12	8–9	9–10	6–7	6–9	9–10	12
A. hebecladoides	9 10	11–12	5–8	7–8	9–12	11–2	3	N.O.
A. Seyal	10–12	10–12	8–9	9–10	Any month			About four months after flowering
A. usambarensis	9–10	11–1	5–9	8–9	12	12–2	2–3	12–1
A. verugera	10	11	5–9	8–9	11	11	12	1–2
Bauhinia Thonningii	12	12	4–5	6	1	1–3	3	10–11
Berlinia globiflora	10–11	11–1	6–7	9–10	2	2–4	3–5	8–10
Brachystegia microphylla	9–10	11	7–8	9–10	10–11	11–12	1	6
Cassia goratensis	10–12	10–12	5	6–7	7–8	8–9	10	12
Dichrostachys glomerata	12	12	N.O.	N.O.	1	2	2–3	3 on
D. nyassana	11–12	12	N.O.	N.O.	11–12	12	1	3 on
Lonchocarpus violaceus	10	11–12	N.O.	N.O.	11	11	12	N.O.
Swartzia Madagascariensis	12	1	10	10–11	11	12	1	3
RUBIACEAE								
Randia Thunbergii	11–12	12	N.O.	N.O.	11	12	1	3
SIMARUBACEAE								
Harrisonia abyssinica	Evergreen as a rule at Kikori				11	11	12	2–3
STERCULIACEAE								
Dombeya reticulata	10	11	6	8	9	9	10	1

as belonging to the "Mbuga" type, are those found in the "Mbuga" stream bed, the "Mbuga," the *Acacia Seyal* ecotone and the *Ac. formicarum* communities. Among the *Combretum* open woodland soil types would be placed the soils of the *Acacia usambarensis*, *Ac. usambarensis-Combretum*-Other spp. ecotone and the *Combretum* open woodland communities. It would appear as though the "Mbuga" soils developed and improved from the stream bed type to the *Acacia formicarum* type. The soils found in the *Ac. usambarensis* community might be derived from the *Ac. Seyal* ecotone soils direct or from the *Ac. formicarum* soils, and eventually develop to the *Combretum* open woodland soils proper.

Conclusions as to the development of plant successions, drawn from examination of data collected in the study of vegetation exposed to and protected from the annual fires, are supported by this suggested derivation of the different types of soils.

The "Mbuga" appears to be a stage following upon pioneer Hydroseral communities which, if continuously protected from fire, gives way to the pioneer *Acacias*—*Ac. Seyal*, *Ac. campylacantha*, etc. These, in turn, are succeeded by the Gall Acacia communities. Deciduous thicket may develop from the Gall Acacia communities direct (see Pl. XIX, Phot. 4, Pl. XX, Phot. 6) or the latter may be succeeded by *Acacia usambarensis*. The *Ac. usambarensis* may give way to *Combretum* open woodland or to deciduous thicket direct (see Pls. XXI, XXII). The *Combretum* open woodland may be succeeded by deciduous thicket which appears to be the climax community of this region.

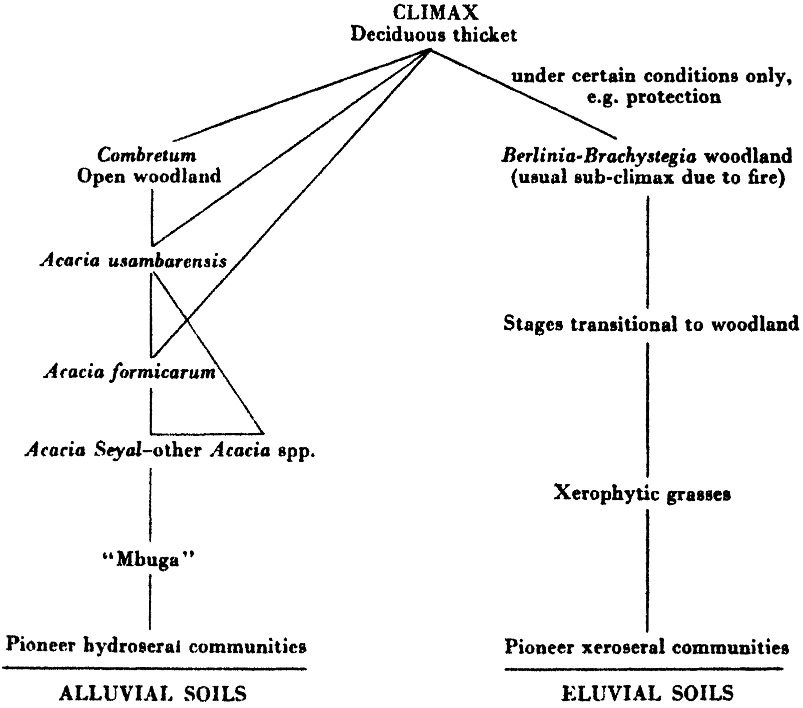

CLIMAX
Deciduous thicket
under certain conditions only, e.g. protection
Combretum
Open woodland
Berlinia-Brachystegia woodland
(usual sub-climax due to fire)
Acacia usambarensis
Stages transitional to woodland
Acacia formicarum
Acacia Seyal–other Acacia spp.
Xerophytic grasses
"Mbuga"
Pioneer hydroseral communities
Pioneer xeroseral communities
ALLUVIAL SOILS
ELUVIAL SOILS

FIG. 9. Schematic chart showing probable plant successions.

From observations over the two years it has been shown that, if the various vegetation communities are protected from fire, there is an enormous thickening up of the vegetation with a reduction in the grasses. Continuous protection from fire would be useless if the lands were wanted for pasturage but it would appear to be of great advantage in the fight against the Tsetse fly. The fast thickening up of the vegetation, the fairly rapid growth of seedlings, suckers, and coppice in most species, but more especially in the thicket-forming plants, and the development of the vegetation towards deciduous thicket (the rate of development depending, of course, on the soils), which does not appear to provide a favourable habitat for the fly (possibly on account of the low light intensity), would be promoted by the protection of these areas from fire.

It is more difficult to draw conclusions in regard to the successions on the eluvial soils. It would appear that the *Berlinia-Brachystegia* communities have developed, through various transitional stages, from the pioneer xeroseral communities. Whether the *Berlinia-Brachystegia* communities are climax, or seral to deciduous thicket, is a moot point. From observations at Kikori, one would suggest that they are *sub-climax* owing to the ever recurring fires but, in protected areas (e.g. the ravine community at Kikori through which the transect was run), they are seral to deciduous thicket.

A chart of the probable successions at Kikori based on that of Phillips (1930) is given in Fig. 9.

SUMMARY.

1. A general account of the main soil types and climatic conditions with seasonal and annual variations is given.

2. The objects of the two years' research and the methods of investigating the habitat conditions (edaphic and aerial) and the development of the vegetation within the principal communities are outlined.

3. The summarised results obtained from the study of the soils, aerial factors, and vegetation, are given for the following vegetation communities:

(*a*) "Mbuga" stream bed.
(*b*) "Mbuga" or seasonal swamp.
(*c*) "Mbuga"-*Acacia* spp. ecotone.
(*d*) *Acacia formicarum.*
(*e*) *Acacia usambarensis.*
(*f*) *Acacia usambarensis-Combretum*-Other spp. ecotone.
(*g*) *Combretum* open woodland.
(*h*) *Berlinia* woodland or "Miombo."
(*i*) Upland *Brachystegia microphylla.*

4. The effects of protecting from fire areas within these communities is described and discussed.

5. The mean annual growth increments in height of seedlings, suckers and coppice, and in girth of the principal tree species over a period of one year, are given in tabular form. A table is given showing the times of production of the first leaves and full foliage, defoliation, and the occurrence of flowers and fruits of the principal tree species at Kikori.

6. Conclusions are given as to the probable derivation of the soils and the probable plant succession at Kikori. These have been drawn by the writer from personal observation and study of the data collected by himself working in close collaboration with the other members of the staff at Kikori.

ACKNOWLEDGMENTS.

The writer wishes to thank Mr C. F. M. Swynnerton, Director of the Department of Tsetse Research and Reclamation, Tanganyika Territory, for permission to use the data collected at Kikori in this paper.

He is also indebted to his co-workers in the Department of Tsetse Research viz. Messrs Potts, Burtt and Moggridge of Kikori, and Mr G. W. St Clair Thompson of Itundwe, for their help, advice and criticism in his particular part of the work.

Above all, he is most grateful to Dr John Phillips, late Deputy Director of the Department of Tsetse Research, now Professor of Botany in the University of the Witwatersrand, who first outlined the programme of work, who suggested that he should write this paper and who has, throughout, been most kind in his guidance and criticism.

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THE VEGETATION OF THE CHILTERN HILLS, WITH SPECIAL REFERENCE TO THE BEECHWOODS AND THEIR SERAL RELATIONSHIPS

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(*With two Figures in the Text.*)

CONTENTS.

PAGE
TOPOGRAPHY AND GEOLOGY 231
RAINFALL AND TEMPERATURE 231
THE INFLUENCE OF MAN ON THE SUCCESSION 234
PART I. THE VEGETATION OF THE ESCARPMENT[1] 235
  General description of the terrain 235
  General description of the vegetation: the juniper and hawthorn seres 235
  Distinguishing characters of the juniper and hawthorn seres . . 237
    Habitat 237
      (1) Aspect, exposure and slope 237
      (2) Soil 238
        (a) Upper and Middle Chalk 238
        (b) Soil depth 239
        (c) Mechanical analysis (including $CaCO_3$ and humus content) 240
        (d) Nitrification 240
    Vegetation 240
      (1) Species exclusive to the hawthorn sere 240
      (2) Average frequency 242
      (3) Constancy 243
      (4) Life form 243
      (5) Height growth of some species common to both seres . . 244
      (6) Ground stratum 245
      (7) The succession 245
    Statistical data 245
  Description and analysis of the juniper and hawthorn seres . . 247
    Scrub—woody plants 247
    The ash consocies 250
    The immature beech consociation 252
    The beech consociation 255
  Comparison and discussion of the spectra of the significant species of the field stratum of the immature and mature sanicle and mercury woods 261
    Interpretation of results 263
  Comparison with similar vegetation in other areas 266
    The succession 266
    General comparisons 268
    Biological spectra 269
  References 270

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[1] Part II, dealing with the vegetation of the plateau, will appear in the next issue of the JOURNAL.

Our knowledge of English beechwoods rests mainly on examples from the South Downs: and the desirability of extending the basis of their characterisation to the similar woods of the Chilterns and Cotswolds is obvious. At the same time an opportunity is afforded of bringing out differences due to local conditions. This paper deals mainly with the beechwoods of the Chilterns and their seral relationships.

The beechwoods of the Chilterns fall mainly in South Oxfordshire and South Buckinghamshire with an extension north-east into Hertfordshire. But only part of this area has been explored. The well-wooded Hampden Estate in Bucks provided the nucleus of the material used, but round this a body of data drawn from as far as Ashridge to the north-east and Watlington to the south-west has been gathered (Map, Fig. 1, p. 232).

TOPOGRAPHY AND GEOLOGY.

The central and main body of the Chiltern Hills crosses the counties of Oxford, Bucks and Herts in a south-west to north-east direction. The hills are formed of chalk whose strata dip at an angle of about 2·3° to the south-east, the outcrop of (Lower), Middle and Upper Chalk forming a steep escarpment facing north-west overlooking the Vale of Aylesbury. Above this plain (alt. about 250 ft.: 76 m.) the hills rise to an average height of about 750 ft. (229 m.), the highest points reached being Coombe Hill above Ellesborough (852 ft.: 260 m.) and the summit above Halton (861 ft.: 262·5 m.).

Behind the escarpment lies an extensive plateau much dissected by dry valleys of varying age, depth and length, forming part of river systems draining into the Thames to the south. At intervals deep valleys or gaps cut through the escarpment, and along these the main lines of communication run. Chalk outcrops appear on the valley slopes, but on the plateau itself the chalk is covered by leached chalk residues and deposits of Pleistocene and Eocene age, believed to be redistributed by glacial action[1]. The protection to the chalk afforded by these deposits preserves the general flatness of the plateau summits—in this respect a contrast to the rolling contours of the South Downs plateau.

The highly calcareous soils derived from the chalk of the escarpment and valley slopes contrast sharply with the acid gravels or heavy loams of the plateau.

RAINFALL AND TEMPERATURE[2].

The annual rainfall varies in different parts of the Chilterns, but on the average that on the plateau (28–32 in.: 711-813 mm.) is a few inches higher than that on the plain below the escarpment (25–8 in.: 635–711 mm.). The mean annual rainfall at Hampden House on the plateau (alt. 695 ft.: 212 m.)

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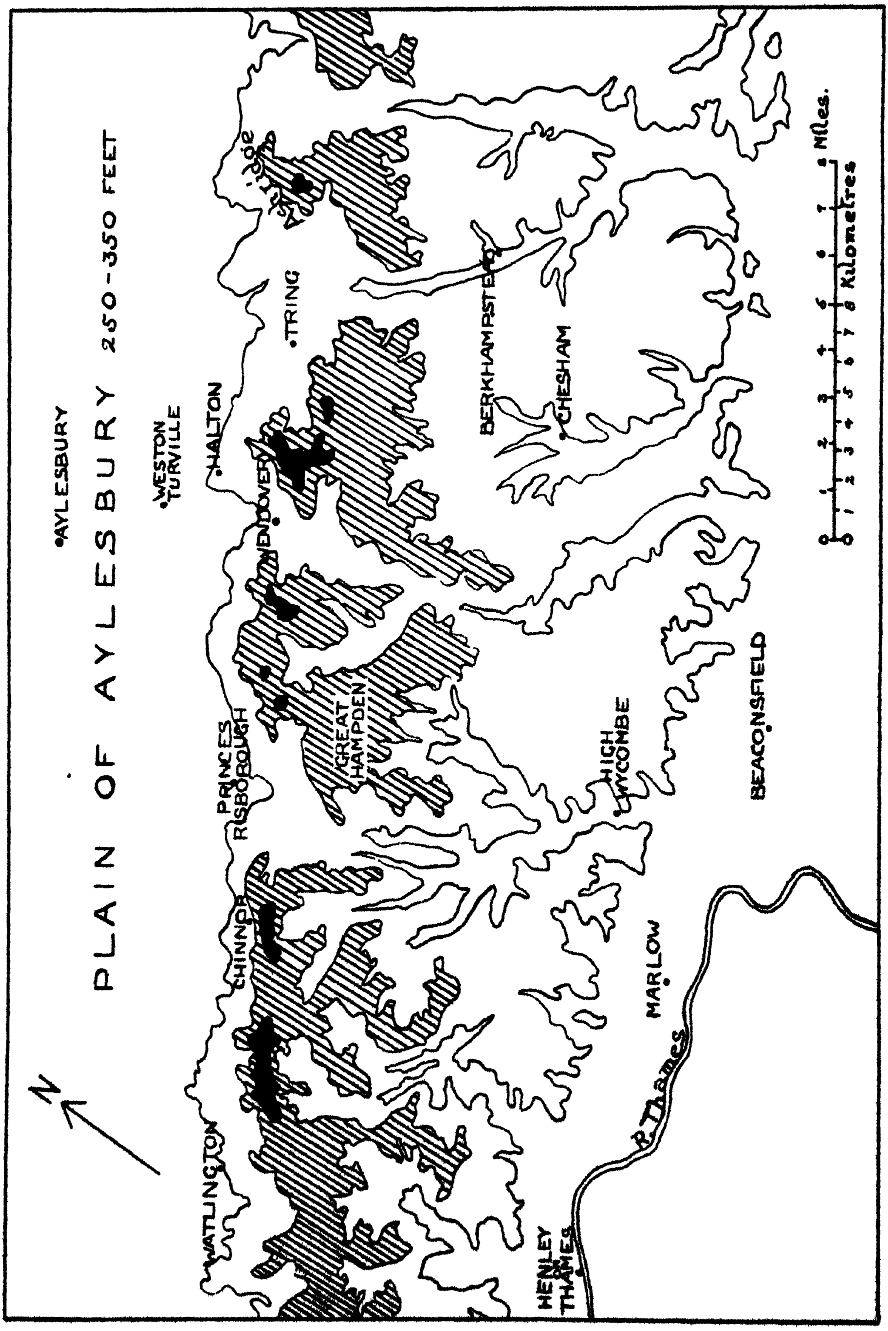
[1] *Mem. Geol. Surv.* No. 238, 1922.

[2] Data from *The Book of Normals*, Sections I, III, and V.


PLAIN OF AYLESBURY 250-350 FEET
AYLESBURY
WESTON TURVILLE
HALTON
TRING
Ashridge
BERKHAMPSTEAD
CHESHAM
WENDOVER
PRINCES RISBOROUGH
GREAT HAMPDEN
HIGH WYCOMBE
BEACONSFIELD
CHINNOR
WATLINGTON
HENLEY ON THAMES
MARLOW
R. Thames
N
0 1 2 3 4 5 6 Miles.
0 1 2 3 4 5 6 7 8 Kilometres

is 30·9 in. (785 mm.), at Little Kimble (alt. 370 ft.: 113 m.), Ellesborough (alt. 400 ft.: 122 m.) and Tring (alt. 401 ft.: 122 m.) on the lower slopes of the escarpment, 28·9 in. (734 mm.), 30·9 in. (785 mm.) and 27·6 in. (701 mm.) respectively; and at Weston Turville (alt. 320 ft.: 98 m.) and Watlington (alt. 325 ft.: 99 m.) on the plain, 25 in. (635 mm.) and 26·7 in. (678 mm.) respectively. Its monthly distribution is shown by the following data from High Wycombe and Berkhamsted:

	High Wycombe (alt. 253 ft.: 77 m.)		Berkhamsted (alt. 450 ft.: 137 m.)	
	in.	mm.	in.	mm.
Jan.	2·09	53	2·34	59
Feb.	1·85	47	2·22	56
Mar.	1·95	50	2·26	57
Apr.	1·57	40	1·81	46
May	1·76	45	1·98	50
June	1·95	50	2·33	59
July	1·97	50	2·46	62
Aug.	2·32	59	2·54	65
Sept.	1·89	48	2·11	54
Oct.	3·13	79	3·57	91
Nov.	2·49	63	2·90	74
Dec.	2·93	74	3·29	84
Total	25·90	658	29·81	757

These data show that April and May are the driest months and October the wettest. Nearly or quite one-third of the precipitation falls in the last quarter of the year, while the spring is decidedly drier, only about one-fifth falling from March to May inclusive.

Compared with the South Downs the maps in the *Book of Normals* show that from October to March the rainfall on the Chilterns is lower, is approximately the same or slightly lower in April, May, July, August and September, but is higher in June. The percentage of the annual total falling during the five months April to August, calculated on the data for High Wycombe and Berkhamsted, is 37·1 and 37·2 respectively. The corresponding figures for Compton House and Ditcham Park in Sussex are 34·5 and 33·3, whilst that for Cambridge is 44·7. Thus as we pass inland from the Sussex coast and towards East Anglia a higher proportion of the annual total falls during spring and summer.

The mean daily maximum and minimum temperatures computed from the maps (*The Book of Normals*, vol. III) show that from March to September the daily maxima on the Chilterns are higher, from November to January lower, while for February and October they are approximately the same as in Sussex. The mean minima, on the other hand, are lower throughout the year on the Chilterns.

FIG. 1. Sketch-map of the central and main portion of the Chiltern Hills. The lowest contour line drawn is that of 400 ft.; 600–800 ft., diagonally hatched; above 800 ft., black. The examples studied lie on the chalk escarpment between Watlington and Ashridge and on the acid soils of the plateau behind at elevations of 600 to over 800 ft.

Thus the rainfall and temperature data show a definite though slight approach to a continental type of climate.

From the study of the vegetation the belief is held that atmospheric humidity (evaporation) is a factor of importance in differentiating the vegetation of the South Downs and Chilterns. Unfortunately no determinations have been made, but on *a priori* grounds the inland area may be expected to have a drier atmosphere than the Sussex Downs, which come immediately under the influence of the prevailing south-west winds from the Channel.

THE INFLUENCE OF MAN ON THE SUCCESSION.

With the important exceptions of the escarpment and the commons on the plateau there exist few or no areas in a natural condition, such as those which enable the ecologist to demonstrate with conviction the details of the plant succession on the South Downs. The free open grasslands and unenclosed woodlands of the Downs are replaced by a patchwork of woodland (almost entirely beechwood) and agricultural land, each with sharp boundaries indicating human control of their limits. Even on the commons, to which examples for the study of succession on the plateau are almost confined, man's influence is felt in ways which sometimes prevent the successful establishment of woody plants. On many, however, control has been relaxed, so that rudiments of the different successional stages may be traced and an outline of the general course is not too difficult to delineate; but the nature and extent of the examples are inadequate for a complete characterisation of the seral units between grassland and climax beechwood. Both these communities owe the maintenance of their present area to human interference, and the sharpness of the break between them is the measure of that control.

Direct evidence on the plant succession receives valuable support from the somewhat scanty historical records available and from old maps where the names given to woodlands are no longer appropriate. Further, while the selection system of woodland management is reputed to have been practised on the Chilterns for several centuries, historical evidence and the evidence from the structure of some of the woodlands suggests that, in some woods at least, little more than a haphazard cutting of timber and firewood from woods of spontaneous origin was practised: and the neglected state of many woodlands, the abandonment of arable cultivation and invasion by woody growth, and the encroachment of woodland upon the broad margins of old roads, now metalled and of narrow width, all testify to the general direction and nature of the succession.

The difficulties experienced in following the succession on the plateau are not met with on the escarpment, for here the vegetation is essentially natural and the different units can readily be related to each other.

The indirect influence of man is exercised chiefly through the pasturing of sheep and cattle on the escarpment and the commons, but the grazing, although of unequal incidence, is on the average not intensive. Rabbits, however, are common, although very unequally distributed: kept down on some estates, they abound on others and the foxes do not seem to be numerous enough to keep them in check. An interesting faunistic change is the replacement of the red squirrel by the grey, which is even more destructive to tree growth.

The account of the vegetation is treated in two parts: Part I deals with the vegetation of the escarpment, Part II with that of the plateau.

PART I. THE VEGETATION OF THE ESCARPMENT.

GENERAL DESCRIPTION OF THE TERRAIN.

The general lie of the escarpment is north-east to south-west, but the straight alignment seen above Chinnor is elsewhere much broken by wind-gaps and projecting spurs enclosing "amphitheatral embayements." Thus while the general aspect is north-west the communities studied actually face in all directions except south-east, although the majority of them are found on slopes facing south-west through west to north. For the same reason the vegetation of the slope is in different parts exposed in different degree to the prevailing south-westerly to westerly winds. The steepness of the escarpment also varies from gentle slopes to a maximum of 34° 50′: but no correlation exists between steepness of slope and exposure to the prevailing winds.

The soft Lower Chalk is mostly under arable cultivation at the foot of the escarpment, the Middle and Upper forming the escarpment itself, where the "Upper Chalk appears as a narrow fringe at the top of the slope and bordering the Clay-with-Flints of the plateau." Actually the brow of the escarpment is covered by non-calcareous deposits, but only the communities on chalk soils have been studied. On weathering, a highly calcareous soil of shallow but varying depth and texture is produced.

GENERAL DESCRIPTION OF THE VEGETATION: THE JUNIPER AND HAWTHORN SERES.

A general view of the escarpment shows communities of scrub and woodland set against a background of grassland. This is particularly true of the southern half of the district, where grassland occupies the largest area, although its grazing value is considerably lessened by the encroachment of scrub. In the northern half the escarpment is much more indented, enclosure of the gentler slopes is fairly frequent, and the area on the whole has the appearance of being more wooded. But the unenclosed parts present a physiognomy similar to the free, open escarpment of the southern half.

The woods, often of no great extent, are almost entirely of beech and occupy habitats of varying aspect, exposure and inclination. It is worthy of note, however, that the bays are often occupied by woodland whilst the adjoining spur slopes bear scrub or grassland: the woodlands of the bays are usually continuous with the woodlands on the plateau above. Even on the straight parts of the escarpment (apart from undoubted planting) beechwood occupies the upper parts of the slope and shows clear evidence of having spread downwards from the woods on the plateau. In other words progress down the slope has proceeded faster in the bays than on the more exposed parts.

Apart from enclosure, direct interference by man is limited. Here and there conifers are planted in small patches. The beechwoods are cut on maturity, either clear or selectively felled, and while the possibility of some of the woods having been planted cannot be entirely excluded, the bulk of them are probably spontaneous. In one locality (on the Clay-with-Flints on the brow of the escarpment) beech is coppiced. Planted and coppiced box is local: but in Green Lawn and Happy Valley (between Little Kimble and Ellesborough) extensive boxwoods of unknown origin exist.

There is no evidence of the early cultivation of the steeper escarpment slopes, but boundary marks and local tradition show that the summits of some of the spurs and the lower slopes of the bays have been cultivated. These areas now bear grassland and colonising scrub.

By the grazing of sheep and rabbits grassland tends to be stabilised, but when the grazing pressure is lifted, either by the withdrawal of sheep or the suppression of rabbits, colonisation by trees and shrubs takes place. Historical records support field observations on this point. The following quotations are from the "Working Plan" of the Hampden Estate and refer to parts of the escarpment slope above Longdown Hill, including Pulpit Hill. "This goes as sheep-run under Longdown Farm, but it includes a lot of timber"; "In Terrier goes as sheep run under Manor Farm, but really is trees"; "In Terrier shown as sheep runs attaching to Manor and Longdown Farms but really is woods," etc. These "sheep runs" now bear grassland, scrub and beechwood.

These observations show that interference by man both directly and indirectly is not of a kind nor exercised to a degree to upset the essential naturalness of the vegetation or the dynamic process of invasion and succession from grassland directly to beechwood or through scrub to beechwood.

The vegetation is similar in essentials to that found on the South Downs escarpment. Chalk grassland is succeeded by a rich calcicolous scrub. Normally ashwood follows, but on the Chilterns examples of an ash consocies are rarely found. In both areas the climax is beechwood, which shows a very sparse shrub layer, a well-developed layer of calcicolous herbs, and a bryophytic layer rich in species.

Closer analysis of the vegetation on the Chiltern escarpment brings out the existence of two parallel seres which we propose to call the juniper and hawthorn seres, from the species respectively dominant in the two kinds of scrub. The corresponding beechwoods may be referred to as the sanicle and mercury beechwoods, from the herbs respectively dominant in the ground vegetation. Briefly summarised the succession is thus:

Juniper sere. Grassland→juniper scrub→beechwood (sanicle).
Hawthorn sere. Grassland→hawthorn scrub→[ashwood]→beechwood (mercury).

The grasslands have not been investigated, but superficial examination shows the existence of two types corresponding with the two seres: grassland dominated by short grasses, of which *Festuca rubra* is the most abundant, and grassland of taller grasses, including *Arrhenatherum elatius*, are referable to the juniper and hawthorn seres respectively.

DISTINGUISHING CHARACTERS OF THE JUNIPER AND HAWTHORN SERES.

Habitat.

In Table I the physical and chemical characteristics of the juniper and hawthorn sere habitats are summarised.

Table I. *Habitat characteristics of the juniper and hawthorn seres.*

	Juniper sere	Hawthorn sere
Exposure to prevailing westerly winds	Generally more exposed	Generally more sheltered
Angle of inclination of slope	Generally on steeper slopes, up to a maximum of 34° 50′	Generally on gentler slopes, up to a maximum of 29°
Chalk horizon	On both Middle and Upper, but typically developed on Upper Chalk or on harder strata	Definite preference for Middle Chalk or on softer strata
Mean soil depth in cm. with extremes in brackets	31 (18–58)	51 (28–76)
Percentage $CaCO_3$ in surface 6 in. of soil in mature beechwood	59·55	33·32
Percentage "loss on ignition" in upper 6 in. of soil in mature beechwood	12·94	23·33
Leaf litter in mature beechwood	Sparse	Forming a layer of 2·5–5 cm. thick
pH values of upper 6 in. of soil in mature beechwoods	7·9	7·6
Soil water relations (by inference)	Smaller water-holding capacity. Less retentive and eustatic	Greater water-holding capacity. More retentive and eustatic
Nitrification (by inference)	Less active	Active

(1) *Aspect, exposure and slope.*

Aspect is found not to be significant.

About one-half of the examples of the hawthorn sere occupy sheltered places, though a clear majority of examples of the juniper sere are found on exposed localities. Thus exposure to the prevailing winds is ruled out as a factor of primary importance in differentiating the seres, but it may, and undoubtedly does, affect the nature of the communities developed. Thus two examples of a well-developed ash consocies and others in an embryonic stage are found in sheltered places only.

General observation connects the juniper sere with steeper and the hawthorn sere with gentler slopes; and this is true for typical examples of each. Measurements show that juniper sere communities grow on slopes with an angle of inclination up to 34° 50′ and those of the hawthorn sere up to 29°. But wide variation exists and exceptional slopes are not necessarily compensated for by other physiographic factors. For example, communities of the hawthorn sere do exist on steep and exposed slopes and examples of the juniper sere on steep and sheltered slopes. Typical examples of the juniper sere do not however occur on gentle and sheltered slopes.

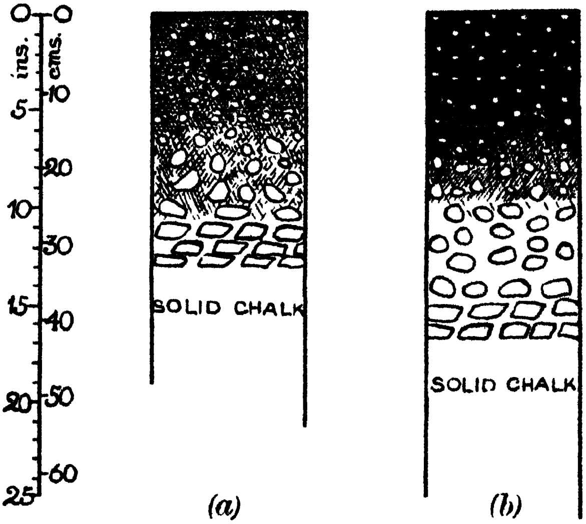


FIG. 2. Sample soil profiles of (*a*) sanicle beechwood and (*b*) mercury beechwood. For details see text, p. 239.

The steepest slope measured on the Chilterns was the detritus slope of a chalk pit, with an angle of 43° 43′. The soil was soft under foot and bore a 50 per cent. cover of herbs and grasses.

(2) *Soil.*

So far as analysed the soils of the two seres show important differences in depth, calcium carbonate and humus contents.

(*a*) *Upper and Middle Chalk.* Neither sere is found to be limited to one geological horizon or the other, but on the whole the hawthorn sere shows a preference for Middle Chalk. The juniper sere is found on both, with some examples on sheltered and some on exposed Middle Chalk. In like manner examples of the hawthorn sere are found, although less often, on sheltered or exposed Upper Chalk. Thus, geological formation as a whole bears no direct relation to the vegetation, but the different horizons, inasmuch as they differ in hardness and ease of weathering, do materially affect the soil, in particular soil depth.

(*b*) *Soil depth.* This appears to be the most important single factor characterising the habitats of the two seres. It is itself the resultant of the interplay of several factors integrating the effects of hardness of the underlying chalk, steepness and exposure of slopes.

Data (from diggings and from chalk pit exposures) have been collected from thirty-six places in the juniper sere and from thirty-two in the hawthorn sere, but in some of the latter there is no sharp transition to hard rock. As the tabulated data show, the average soil depth is less in the juniper sere than in the hawthorn sere by about 20 cm. Examples show the following strata in the profile (Fig. 2).

Juniper sere. In sanicle beechwood, aspect west, sheltered, angle of inclination 32° 20′.

Soil horizon	Depth from surface	Description of soil horizon
A_0	1 in.–0 (2·5 cm.–0)	Litter scattered, variable in depth
A	0–6 in. (0–15 cm.)	Humus darkened, with many small chalk stones and a few flints
	6–11 in. (15–27·5 cm.)	Continuation of above with more earthy material. Brown-black. Larger chalk stones
	11–13 in. (27·5–32·5 cm.)	Angular chalk stones with soft chalk between
C	At 13 in. (33 cm.)	Fissured chalk rock

Hawthorn sere. In mercury beechwood, aspect north-west, partly exposed, angle of inclination 18°.

Soil horizon	Depth from surface	Description of soil horizon
A_0	1 in.–0 (2·5 cm.–0)	Litter continuous
A	0–7·5 in. (0–19 cm.)	Dark, almost black soil with many small chalk stones and a few flints
	7·5–10 in. (19–25 cm.)	Chalk stones with humus-coloured soil between
	10–17 in. (25–43 cm.)	Chalk stones with soft chalk between
C	At 17 in. (43 cm.)	Fissured chalk rock

Other examples show a compact or soft parent rock in the juniper and hawthorn seres respectively.

In the beechwoods the difference in the thickness and continuity of the leaf litter covering is connected with the steepness and/or exposure of the slopes and has an important effect upon the development of the ground stratum of bryophytes. It may be added that the soil of the juniper sere is firmer under foot than that of the hawthorn sere, which is yielding.

(*c*) *Mechanical analysis*[1] (*including* $CaCO_3$ *and humus content*). Six inch samples of "fine soil" from a sanicle and a mercury beechwood yield the following data:

	Juniper sere %	Hawthorn sere %
Moisture in air-dry soil	4·05	6·76
Coarse sand	0·99	1·01
Fine sand	4·05	5·59
Silt	2·18	6·06
Fine silt	8·65	7·19
Clay	3·50	12·01
$CaCO_3$	59·55	33·32
Loss on ignition	12·94	23·33
Loss in solution	3·26	3·80
Total	99·17	99·07
(Stones and gravel	28·94	38·94)

The two soils differ mainly in their contents in $CaCO_3$, humus and clay. The higher clay and humus content, together with greater soil depth, make the soils of the hawthorn sere more retentive of moisture, with a higher moisture-holding capacity. They are thus less liable to dry out during the summer than the shallower, highly calcareous soils of the juniper sere.

(*d*) *Nitrification.* No determinations have been made, but the complex of soil factors in the hawthorn sere more nearly approaches the optimum for this process. The greater frequency and ranker growth of nitratophilous species—*Urtica dioica*, *Epilobium angustifolium*, *Geum urbanum*, *Mercurialis perennis*, *Sambucus nigra*, *Fraxinus excelsior*—support this conclusion.

Vegetation.

(1) *Species exclusive to the hawthorn sere.*

The two seres are closely allied and most of the species are common to both. The following eleven, unrecorded from the juniper sere, are found in two or three woodland communities of the hawthorn sere: *Arrhenatherum elatius*, *Campanula trachelium*, *Dryopteris filix-mas*, *Poa trivialis*, *Pteridium aquilinum*, *Ranunculus repens*, and the ruderals *Carduus crispus*, *Cerastium vulgatum*, *Cirsium arvense*, *Epilobium parviflorum*, *Verbascum thapsus*. No significant species is exclusive to the juniper sere.

The distinctive physiognomies are therefore due to differences in frequency, life form, etc., of the significant species. Species with an average frequency of 2·1 or over[2], constancy 4 or 5, together with those exclusive to the hawthorn sere are considered significant in the field stratum of the beechwoods, and are listed on this and the next page. They are arranged in three groups: (1) those having relatively equal values in both seres, (2) those with significantly higher values in the juniper sere, and (3) those with significantly higher values in the hawthorn sere. In giving judgment on each species account has been taken of the fate of the species during the development of the wood to maturity, and species with decreasing values in the mercury wood with at the same time increasing values in the sanicle wood are relegated to the latter (e.g. *Asperula odorata*, *Brachypodium silvaticum*). Reference has also been made to the field records and "l." is attached to the average frequency values where the species is exclusively local in one or more examples. Also where the constancy is low the number of examples in which the species is recorded is given in brackets. By making allowance for these, rigid adherence to arithmetical averages, which obscure facts of significance and imply a precision not warranted by the field methods used, is avoided and a truer picture presented.

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[1] Determined by the official method for the mechanical analysis of soils. *Agricultural Progress*, 1926.

[2] For the purpose of distinguishing the two seres the immature and mature beechwoods of each sere have been taken as one unit. The average frequency and constancy values given here are got from eighteen examples of the juniper sere (four immature and fourteen mature beechwoods) and twenty-two examples of the hawthorn sere (thirteen immature and nine mature beechwoods). This procedure has obvious drawbacks, but it avoids contrasting values obtained from very unequal numbers of examples in the same stage of development.

To obtain the average frequency of species in the two seres the scale commonly used in this country has been translated into figures (d. = 5, a. = 4, f. = 3, o. = 2, r. and l. = 1: a qualifying "l." reduces the value by 1).

List of field layer species in the sanicle and mercury beechwoods with constancies of 4 *and* 5 *and/or average frequencies of* 2·1 *and over, together with species occurring in both the immature and mature mercury woods and exclusive to the hawthorn sere.*

		Juniper sere						Hawthorn sere					
		Immature beech consociation		Mature beech consociation		Immature and mature beech consociation		Immature beech consociation		Mature beech consociation		Immature and mature beech consociation	
No. of examples		4		14		18		13		9		22	
Life form‡		C.*	A.F.†	C.*	A.F.†	C.*	A.F.†	C.*	A.F.†	C.*	A.F.†	C.*	A.F.†
	Group (1). Species with relatively equal values in both seres.												
H.r.	Fragaria vesca	3	2·5	5	2·8	5	2·7	5	2·6	5	2·2	5	2·4
H.r.	Viola hirta	4	1·3	5	1·7	5	1·6	4	1·8	4	1·7	4	1·8
H.r.	Primula vulgaris	3	2·0	3	2·3	3	2·2	4	1·8	4	1·4	4	1·7
H.r.	Oxalis acetosella	(1) 2	l. 1·0	3	1·9	3	1·8	2	2·4	2	1·7	2	2·1
H.s.	Arctium minus	(1) 2	2·0	4	1·9	4	1·9	3	1·9	4	2·0	4	1·9
H.s.	Senecio jacobaea	—	—	4	1·8	3	1·8	3	2·0	4	2·1	3	2·1
H.c.	Milium effusum	(1) 2	2·0	(2) 1	1·5	(3) 1	1·9	(2) 1	2·3	(1) 1	l. 1·0	(3) 1	1·9
T.	Geranium robertianum	3	2·0	2	2·2	2	2·1	5	2·0	3	1·8	4	1·9
	Group (2). Species with significantly higher values in the juniper sere.												
H.r.	Sanicula europaea	5	2·5	5	4·3	5	3·9	2	2·5	3	1·9	2	2·2
H.r.	Viola silvatica§ (agg.)	4	2·2	5	3·2	5	3·0	5	2·5	5	2·3	5	2·4
H.r.	Taraxacum officinale	2	2·0	3	1·9	3	1·9	2	l. 1·0	—	—	1	l. 1·0
H.s.	Campanula rotundifolia	2	2·0	4	1·8	3	1·8	2	l. 1·0	—	—	1	l. 1·0
H.s.	Lactuca muralis	4	2·0	5	2·1	5	2·1	3	2·0	2	2·0	2	2·0
H.c.	Bromus asper	4	2·3	4	2·2	4	2·2	2	1·8	2	1·7	2	1·8
H.c.	Festuca rubra	2	2·0	4	2·1	4	2·0	2	l. 1·3	—	—	1	l. 1·3
H.c.	Brachypodium silvaticum	4	2·3	5	2·1	5	2·1	5	2·0	3	1·8	4	1·9
H.c.	Deschampsia caespitosa	3	2·0	4	2·0	4	2·0	3	2·1	2	1·7	3	2·0
G.r.	Cephalanthera grandiflora	5	2·0	4	2·1	4	2·0	2	2·0	2	1·8	2	1·9
G.r.	Neottia nidus-avis	—	—	4	1·8	3	1·8	2	1·3	(1) 1	l. 1·0	1	1·3
G.r.	Carex glauca	2	2·0	4	2·1	4	2·1	2	l. 1·7	—	—	1	l. 1·7
G.r.	Helleborine latifolia	—	—	4	2·1	3	2·1	1	2·3	2	2·0	1	2·1
G.r.	Asperula odorata	3	2·5	5	2·6	5	2·6	4	2·4	3	1·4	4	2·0
G.r.	Anemone nemorosa	—	—	2	2·8	2	2·8	2	1·7	2	2·5	2	1·8
G.rad.	Monotropa hypopitys	3	2·0	4	2·0	4	2·0	2	2·0	2	1·5	2	1·8

* Constancy. † Average frequency.

‡ Raunkiaer's life forms as subdivided by Braun-Blanquet, *Pflanzensoziologie*, 1928: Ch. = chamaephytes; H.r., H.s., H.c. = hemicryptophyta rosulata, scaposa and caespitosa respectively; G.r., G.rad., G.b. = geophyta rhizomata, radicigemma and bulbosa respectively; T. = therophytes.

§ Mostly *V. silvestris*.

		Juniper sere						Hawthorn sere					
		Immature beech consociation		Mature beech consociation		Immature and mature beech consociation		Immature beech consociation		Mature beech consociation		Immature and mature beech consociation	
	No. of examples	4		14		18		13		9		22	
		C.*	A.F.†	C.*	A.F.†	C.*	A.F.†	C.*	A.F.†	C.*	A.F.†	C.*	A.F.†
	Group (3). Species with significantly higher values in the hawthorn sere.												
Life form‡													
Ch.	Veronica chamaedrys	2	2·0	3	1·7	2	1·7	3	1·9	5	2·0	4	1·9
Ch.	Lamium galeobdolon	—	—	2	1·7	1	1·7	3	2·5	3	l. 1·7	3	2·1
Ch.	Nepeta glechoma	—	—	(1) 1	l. 1·0	(1) 1	l. 1·0	2	3·0	2	2·0	2	2·5
Ch.	Cerastium vulgatum	—	—	—	—	—	—	(1) 1	l. 1·0	(1) 1	2·0	(2) 1	1·5
H.r.	Dryopteris filix-mas	—	—	—	—	—	—	2	2·0	3	1·4	3	1·7
H.r.	Potentilla reptans	—	—	(2) 1	l. 1·0	(2) 1	l. 1·0	(2) 1	l. 2·5	(2) 2	l. 1·0	(4) 1	l. 1·8
H.s.	Mercurialis perennis	(1) 2	l. 1·0	5	2·3	4	2·2	5	3·4	5	4·3	5	3·8
H.s.	Urtica dioica	—	—	2	l. 3·3	1	l. 3·3	4	2·7	5	2·9	5	2·8
H.s. (G.r.)	Epilobium angustifolium	2	2·0	2	2·3	2	2·2	4	2·1	4	2·7	4	2·3
H.s.	E. montanum	3	2·0	3	1·9	3	1·9	4	2·1	4	2·0	4	2·1
H.s.	Geum urbanum	3	2·0	3	1·9	3	1·9	5	2·1	4	2·0	4	2·1
H.s.	Scrophularia nodosa	—	—	2	1·7	1	1·7	2	1·8	5	1·7	3	1·8
H.s.	Ajuga reptans	—	—	3	1·6	2	1·6	2	2·0	4	1·8	3	1·9
H.s.	Carduus crispus	—	—	—	—	—		(1) 1	2·0	(2) 2	1·8	(3) 1	1·8
H.s.	Campanula trachelium	—	—	—	—		—	2	1·8	2	2·0	2	1·9
H.s.	Epilobium parviflorum	—	—	—	—	—		1	2·0	2	2·0	2	2·0
H.s.	Ranunculus repens	—	—	—	—	—	—	2	1·6	3	1·8	2	1·7
H.s.	Verbascum thapsus	—	—	—			—	2	l. 1·0	1	l. 1·0	1	l. 1·0
H.c.	Agrostis alba	—	—	(1) 1	l. 1·5	(1) 1	l. 1·5	2	2·2	2	2·2	2	2·2
H.c.	Hordeum silvaticum	—	—	1	1·5	1	1·5	1	2·5	1	2·0	1	2·3
H.c.	Arrhenatherum elatius	—	—	—	—	—	—	1	2·0	1	2·0	1	2·0
H.c.	Poa trivialis	—	—	—	—	—	—	1	2·0	3	1·5	2	1·7
G.r.	Circaea lutetiana	(1) 2	l. 2·0	(2) 1	l. 2·0	(3) 1	l. 2·0	3	2·1	5	2·2	1	2·1
G.rad.	Cirsium arvense	—	—	—	—	—	—	(1) 1	l. 1·0	(3) 2	l. 1·7	(4) 1	l. 1·5
G.b.	Arum maculatum	—	—	2	2·0	1	2·0	2	2·1	3	2·0	3	2·1
T.	Galium aparine	(1) 2	l. 2·0	(1) 1	l. 2·0	(2) 1	l. 2·0	4	2·2	4	1·8	4	2·0
T.	Myosotis arvensis	—	—	1	1·0	1	1·0	2	1·7	1	1·8	3	1·8

* Constancy. † Average frequency.

‡ Raunkiaer's life forms as subdivided by Braun-Blanquet, *Pflanzensociologie*, 1928: Ch. = chamaephytes; H.r., H.s., H.c. = hemicryptophyta rosulata, scaposa and caespitosa respectively; G.r., G.rad., G.b. = geophyta rhizomata, radicigemma and bulbosa respectively; T. = therophytes.

(2) *Average frequency.*

The majority of the species have low average frequencies (2·0 and under) and those few with outstanding differences in their frequency values confer distinctive appearance on the communities of the two seres.

Juniperus communis (juniper sere, 4·2; hawthorn sere, 2·5) and *Crataegus monogyna* (juniper sere, 2·2; hawthorn sere, 3·7) are the most frequent in the respective scrubs, as are *Sanicula europaea* (juniper sere, 3·9; hawthorn sere, 2·2) and *Mercurialis perennis* (juniper sere, 2·2; hawthorn sere, 3·8) in the ground vegetation of the beechwoods of each sere. Not only so but their average frequencies in the contrasted seres are significantly lower. With the exception of *Nepeta glechoma* (juniper sere, 1·0; hawthorn sere, 2·5), which is essentially a species of developing beechwoods, no other species shows a difference of like magnitude. But the species of group (2) have on the whole slightly higher values in the sanicle wood, and those of group (3) higher values in the mercury wood.

The frequencies of the bryophytes are unfortunately not complete. But in the sanicle woods mosses and liverworts are much more in evidence than in the mercury woods, and where differences in the average frequencies are noted, the values for the sanicle woods are, with few exceptions, higher.

Among woody species which persist in the successive communities of the seres, attention is drawn to the slight but consistently higher average frequencies of *Hedera* and *Ilex* in the juniper sere and of *Fraxinus* in the hawthorn sere.

(3) *Constancy.*

In contrast to the small number of species with high average frequency the number with high constancy is large. But both in scrub and beechwood the majority of species have similar constancy values.

In scrub *Taxus baccata* (5 in the juniper sere; 2 in the hawthorn sere), *Ilex aquifolium* (4 and 2), *Tamus communis* (4 and 2) and *Rosa micrantha* (3 and 1) have significantly higher constancies in the juniper sere, whilst *Euonymus europaeus* (1 and 3) has the higher value in the hawthorn sere.

In the beechwoods the species of group (2) have in general significantly higher constancies in the sanicle wood, and of group (3) higher values in the mercury wood. To these may be added *Sambucus nigra* with 2 in the sanicle and 5 in the mercury wood.

Some of the bryophytes show a fairly sharp contrast. *Dicranum scoparium* (4 in the juniper sere; 2 in the hawthorn sere), *Mnium hornum* (4 and 2), *Plagiochila asplenioides* (4 and 2), *Anomodon viticulosus* (3 and 1), *Brachythecium glareosum* (3 and 1), and *Neckera crispa* (3 and 1) have significantly higher values in the juniper sere, whilst *Fissidens taxifolius* (3 and 5) is the only bryophyte with similar pre-eminence in the hawthorn sere.

(4) *Life form.*

The evergreen xerophyte juniper characterises the juniper scrub: the hawthorn scrub by contrast is summer green.

The spectra of significant species of the beechwoods present several contrasts, but the salient differences only are emphasised here. Fuller discussion will be found on p. 261:

	Ch.	H.r.	H.s.	H.c.	G.r.	G.rad.	G.b.	T.	Total
Sanicle wood									
From group (2)	0	3	2	4	6	1	0	0	16
„ (1)	0	4	2	1	0	0	0	1	8
	0	7 (29)	4 (17)	5 (21)	6 (25)	1 (4)	0	1 (4)	24 (100)
Mercury wood									
From group (3)	4	2	12	4	2	1	1	2	28
„ (1)	0	4	2	1	0	0	0	1	8
	4 (11)	6 (17)	14 (39)	5 (14)	2 (5)	1 (3)	1 (3)	3 (8)	36 (100)

The most striking single feature of these spectra is the lack of pre-eminence of any one life form in the sanicle wood and the definite maximum of hemicryptophyta scaposa in the mercury wood. This characteristic spectrum of the mercury wood is due to the tall, social habit and long maintained leaves of mercury which excludes or tends to exclude species the average level of whose leaves is nearer the soil surface, whether these species belong to the same life-form class or not. Thus rosette hemicryptophytes and short-stemmed geophytes like *Asperula odorata* tend to be excluded, as shown by the decreasing constancy and/or average frequency values in the mature as compared with the immature mercury wood, whilst at the same time increasing values are shown in the corresponding sanicle woods. Similarly the large-leaved rosette hemicryptophyte, *Dryopteris filix-mas*, and the tall-growing rhizome geophytes, *Circaea lutetiana* and *Epilobium angustifolium*, with height and shoot form similar to *Mercurialis*, maintain their position in the mature mercury wood. The other rhizome geophytes—*Cephalanthera grandiflora*, *Neottia nidus-avis*, *Helleborine latifolia*, *Carex glauca*, *Anemone nemorosa* and the saprophytic geophyte with root buds *Monotropa hypopitys*—characterise the sanicle wood.

The same feature emerges from a study of the spectra of species exclusive to each sere and found in one or more of the seral communities. Many of these are not woodland plants but relicts from grassland.

	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	G.rad.	T.	Total
Juniper sere	1	4	3	0	2	0	0	0	10
Hawthorn sere									
In one community only	1	1	11	5	1	1	0	2	22
In more than one	1	1	5	2	1	0	1	0	11
(spp. on p. 240)									
	2	2	16	7	2	1	1	2	33

Since the bulk of the species grow in either sere it is concluded that the hemicryptophyta scaposa (in particular) find the habitat of the sanicle wood less than optimal, and that the species characteristic of the sanicle wood find a refuge here from the competition of taller life forms.

(5) *Height growth of some species common to both seres.*

Average height growth in feet (with extremes in brackets) of certain species in the juniper and hawthorn seres.

	Juniper sere	Hawthorn sere
Juniperus communis	4–5 (1·5–6)	8-10 up to 15
Crataegus monogyna	Up to 9	Up to 18
Fagus silvatica	67 (54–77)	77 (70–85)
Fraxinus excelsior	Similar to beech	Similar to beech
Mercurialis perennis	0·5	1·25 (0·75–1·7)

For these species (as well as for some others not measured) the habitat of the hawthorn sere is more favourable to growth. This is true even of the juniper, although in the hawthorn sere its foliage is paler in colour.

In the hawthorn sere the beech grows faster, has taller, straighter stems and usually smoother bark than in the juniper sere. The height attained probably excludes *Sorbus aria* from the canopy of the mercury beechwood.

The ash also grows faster in the hawthorn sere, and sapling ash has a greener, smoother and more lush bark. Forking of the stems due to the death of the terminal buds is found in both seres, but is more noticeable in the more slowly grown trees of the juniper sere. The difference in the rate of growth may contribute to this effect.

The difference in the height of *Mercurialis* is accompanied by differences in density and colour. In the mercury wood, *Mercurialis* is dark green and forms dense masses; in the sanicle wood it is a small plant, with pale green leaves, and sparse.

(6) *Ground stratum.*

The difference in the height and density of the field stratum and in the thickness of the leaf litter accounts for the better development of the ground stratum of bryophytes in the sanicle than in the mercury wood.

(7) *The succession.*

The outstanding difference in the succession is the inclusion of an ash consocies in the hawthorn sere. Although the difference in the average frequency of ash in the beechwoods of the two seres is not great, in well-sheltered places the beginnings of an ash consocies are quite definite. Its development is much hindered and in places even prevented by rabbit attack.

These differences emphasise the conclusion reached respecting the habitats of the two seres. The vegetation of the juniper sere is more xerophytic, that of the hawthorn sere more mesophytic. Furthermore hawthorn and mercury and associated herbs which characterise the hawthorn sere are excluded as significant species from the juniper sere on edaphic grounds: from the hawthorn sere, juniper and sanicle are or tend to be excluded by competition with taller growing species.

Statistical data.

The two sets of data tabulated below demonstrate some of the characteristics of the two seres. The data illustrate the dominance of rosette hemicryptophytes and of hemicryptophytes with leafy flowering stems in the sanicle and mercury wood respectively, and the relation of mercury of different densities and heights to the presence and frequency of other species of low-growing form, even although, as in *Asperula odorata*, the habitat may be more favourable to their growth. In the intermediate sanicle-mercury examples the species typical of the sanicle wood are either excluded or reduced in number, and their places may be taken by species more commonly found in the mercury wood.

Sanicle and mercury beechwoods.

Data of some habitat factors, species, number of individuals of each species, and height of *Mercurialis perennis* from one square metre, in typical examples of the sanicle and mercury beechwood, and in a beechwood intermediate between these two.

Type of mature beechwood	Sanicle	Sanicle-mercury	Mercury
Habitat			
Aspect	West (sheltered)	West (exposed)	North-west (partly sheltered)
Angle of slope	32° 20′	23° 40′	18°
Thickness of litter	Variable 0–1 in.	Variable 0–1 in.	1 in.
Depth of soil	13 in.	18 in.	17 in.
Species, life form and number of individuals.			
H.r. Sanicula europaea Adults	133	35	0
Seedlings	206	18	0
H.r. Viola silvestris Adults	45	34	0
Seedlings	6	17	0
Ch. Hedera helix (rooting parts)	15	0	0
G.r. Asperula odorata	9	0	0
H.c. Bromus asper	2	0	0
H.s. Lactuca muralis	1	0	0
H.r. Primula vulgaris	0	8	0
G.r. Anemone nemorosa	0	5	0
Ch. Lamium galeobdolon Adults	0	3	0
Seedlings	0	2	0
H.s. Ajuga reptans	0	2	0
Ch. Euphorbia amygdaloides	0	1	0
H.s. Mercurialis perennis	0	93	259
Fraxinus excelsior—seedlings	53	2	0
Fagus silvatica—seedlings	5	0	0
Prunus avium—seedlings	2	0	0
Eurhynchium striatum	4	0	0
Total number of species	10	9	1
Average height in in. of *Mercurialis* (extremes in brackets)	—	6·4 (2·5–8·8)	9·5 (3·5–13·5)

Data of species, number of individuals and height of *Mercurialis perennis* and *Asperula odorata* from 3 sq. ft. (3 × 1) from different facies in the same beechwood. Angle of slope 9° 20′.

Facies in beechwood	Sanicle	Sanicle-mercury	Mercury
H.r. Sanicula europaea	34	26	0
H.r. Viola hirta Adults	12	0	0
Seedlings	1	0	0
H.r. V. silvatica (agg.) Adults	13	0	0
Seedlings	1	0	0
H.r. Fragaria vesca	13	0	0
G.r. Asperula odorata	1	4	0
H.s. Mercurialis perennis Adults	2	20	140
Seedlings	0	2	0
Fraxinus excelsior—seedlings	2	0	0
Total number of species	7	3	1
Average height in in. of *Mercurialis* (extremes in brackets)	3	7·2 (4·8–9·0)	9·5 (2·0–17·0)
Average height in in. of *Asperula* (extremes in brackets)	4	5·4 (3·8–7·0)	—

DESCRIPTION AND ANALYSIS OF THE JUNIPER AND HAWTHORN SERES.

Scrub—woody plants.

Typical examples of juniper scrub and hawthorn scrub are quite distinct, and in ungrazed areas the dominant species in each finds the habitat of the other less than optimal. Hawthorn, for example, is never more than occasional in typical juniper scrub, and, while juniper attains large dimensions and occasionally a high frequency in hawthorn scrub it does not show the healthy green observed in the type community (**8**). Again in some ungrazed areas local soil inequalities bring out the salient difference, for juniper is more frequent on the shallower soil of the ridges while hawthorn dominates in the hollows and on gentler slopes. Here of course the more light-demanding juniper fails to hold its own with hawthorn.

Ten examples each of juniper scrub and hawthorn scrub have been investigated. Forty-eight species are recorded from the juniper scrub and forty-five from the hawthorn, of which forty-two are common to both. Those recorded from one only are of no significance, accidental or alien. The species therefore are essentially the same in both.

Except for the two dominants all the species are of relatively low frequency. Taking both scrub communities together *Juniperus* has a higher average frequency (4·2) than *Crataegus* (3·7) and, in the hawthorn sere, juniper has a somewhat higher frequency (2·5) than hawthorn has in the juniper sere (2·2). The only other species showing a noticeable difference is *Prunus spinosa* (2·1 in the juniper sere, 2·8 in the hawthorn sere), but its frequency varies much in the examples of both seres.

Strongly contrasted with the frequencies the number of species with high constancy is large. Ten species have constancy 5 in both seres: *Cornus sanguinea*, *Crataegus monogyna*, *Fagus silvatica*, *Ligustrum vulgare*, *Prunus spinosa*, *Rhamnus catharticus*, *Rosa canina*, *Rubus fruticosus* (agg.), *Sorbus aria*, *Viburnum lantana*. Besides these (and of course juniper) *Taxus* has the highest figure in the juniper sere (2 in the hawthorn sere) and *Fraxinus* the highest figure in the hawthorn sere (4 in the juniper sere). *Corylus*, *Prunus avium* and *Sambucus* have the value 4 in each sere and *Acer pseudoplatanus* and *Bryonia* 4 in the juniper sere and 3 in the hawthorn sere. Greater differences are shown by *Ilex*, *Solanum* and *Tamus* (4 in the juniper sere and 2 in the hawthorn sere) and *Rubus caesius* (2 and 4). Among species (excluding conifers) of lower constancy, *Sorbus aucuparia* and *Rosa micrantha* have the value 3 in the juniper sere and 1 in the hawthorn sere, whilst *Euonymus* has 1 and 3 respectively.

The vast majority of the species (forty-three and forty-one respectively) are phanerophytes, very few (four and three respectively) being hemicryptophytes. The only geophyte is *Tamus communis*.

In both seres juniper is represented by the columnar and the spreading form: the latter is the more frequent. In typical examples of the juniper sere, its average height is about 4 ft. (1·2 m.) reaching in closed scrub to 6 ft. (1·8 m.). There is however much variation. On the shallow soil of steep exposed slopes, juniper is from 18 in. to 24 in. (45–60 cm.) high: in sheltered places with deeper soil (fragments of the hawthorn sere) it may attain 12 ft. (3·60 m.). Generally speaking, at the foot of slopes the shrubs are larger and denser. Again, juniper bushes cut over (e.g. in shooting rides) have their adventitious shoots cropped close by persistent rabbit nibbling.

The prevailing westerly winds have a noticeable but not a marked effect on the form of the scrub constituents.

The bulk of the scrub is more or less open, closed examples being more commonly found in the juniper sere, whilst hawthorn scrub is typically open with local impenetrable masses of no great extent. This density is apparently correlated with severity of grazing, for when the pressure is lifted the intervals between the scattered old bushes (mostly junipers) are colonised by hawthorn, or juniper and hawthorn together, coming up among the ungrazed grass. A later stage of a colonisation of this kind is seen on Lodge Hill (above Bledlow), where locally the juniper is being suppressed by a mass of blackthorn. Usually *Prunus spinosa* forms thickets, evidently the result of vegetative reproduction. On disturbed soil, *Sambucus* forms societies of varying extent. The other species play a subordinate part. *Corylus* is sparse on steep slopes but becomes more prominent on deeper soil at the foot, and *Cornus* with *Viburnum lantana* are locally pioneers in abandoned pastures, but are unimportant constituents of scrub.

While most of the species of calcicolous coppice are present it is unlikely that cutting of the scrub would lead to a multiplication of "coppice species," and in this connection it is worthy of notice that while oak-hazel coppice is found—although sparingly—on the plateau, no calcicolous coppice (except beech and box—both very fibrous-rooted plants) occurs on the escarpment. This is in striking contrast to the South Downs, where at least in the depressions of the escarpment calcicolous coppice is found.

This similarity of the two scrubs in floristic composition, constancy and frequency of species, is due to grazing. Except *Sambucus* none of the more prominent shrubs is immune from the grazing of animals, shoots being eaten and stems barked. (In one locality only was "top-grazing" seen done during the summer—as recorded from the South Downs (8), the species nibbled being *Prunus spinosa.*) But while nearly all species are attacked, they do not suffer in the same degree, and this selective effect leads to the prominence of the more resistant. Hence while juniper dominates in juniper scrub, the less resistant hawthorn in the hawthorn scrub is kept down and the junipers present stand out. This process may be carried so far that potential hawthorn scrub may be replaced by a community, either open or closed, of *Juniperus* with or without *Sambucus*, a community which under heavy rabbit pressure fails to maintain itself and retrogresses to grassland. This is confirmed by a gamekeeper, who tells me that juniper is disappearing from a certain very open scrub, also belonging to the hawthorn sere, but consisting of occasional hawthorn, locally dominant *Sambucus*, and scattered, large, decrepit, living and dead junipers.

Trees in scrub. The following trees are found in scrub: *Fagus silvatica, Quercus robur, Fraxinus excelsior, Carpinus betulus, Pinus silvestris* (subspontaneous), *Sorbus aria, S. aucuparia* and *Taxus baccata.* Of wood-formers *Fagus* is the most successful: next in order and much behind come *Fraxinus, Quercus, Carpinus* and *Pinus.*

Beech occurs in all the examples with an average frequency of about 2·5. All ages are represented, with the younger predominating, occasionally in fairly large even-aged groups, but many really old trees are kept down by grazing. The prevailing winds cause the formation of a lop-sided crown only in the most exposed places, and even in exposed juniper scrub isolated trees up to 15 ft. (4·5 m.) maintain an erect leading shoot.

In both scrubs ash combines a high constancy value (4 and 5) with low average frequency (1·8 and 1·9) and this frequency is increased only in sheltered places in the hawthorn sere. The ash suffers from the attacks of a number of enemies. Young plants are grazed by rabbits and older saplings are crippled by persistent nibbling of the bark. The stems are often covered and indented by the attacks of *Chionaspis salicis*: the terminal buds are frequently killed by *Prays curtisellus*, leading to forking of the main stem and lateral branches; and the shoots are sometimes cankered by *Nectria galligena.* But inorganic factors appear also to be hostile, for the rate of growth is slow—an extreme example grown under full light conditions having a height growth of 8 in. (20 cm.) only in 20 years. The wind has little effect on the crown form even of examples growing to a height of 20 ft. (6·1 m.). Exceptionally in the hawthorn scrub, as in the sheltered valley at Wainhill, ash sapling invaders are present in quantity. Many have maintained their leading shoots, although forking does occur, and but for the severe rabbit damage to the stems this community has the makings of an ash consocies.

On the escarpment *Quercus robur* is the only species of oak recorded. With constancy 3 in both seres, it has an average frequency of 1·2 and 2·0 in the juniper and hawthorn sere respectively. It is found as seedlings or small trees up to 10–12 ft. (3–3·6 m.). Seedlings, although widespread, are not common and their failure to survive, due in part at least to grazing, precludes the oak from playing any part in the development of the vegetation.

Carpinus (constancy 3 and 2 and average frequency 1·5 and 1·7 in the juniper and hawthorn sere respectively) is chiefly, although not exclusively, local. Where it occurs it is apparently derived from boundary trees.

Older pines are sporadic and subspontaneous young trees grow in their neighbourhood. But occasional young pines are found at considerable distances from the nearest seed-bearing trees. *Sorbus aria* has a high constancy (5) and a relatively high frequency (2·4 in the juniper sere, and 2·2 in the hawthorn sere), but *Sorbus aucuparia* is an occasional to rare constituent which in the juniper sere may grow to 25 ft. (7·6 m.)[1].

Taxus with constancy 5 in the juniper sere and 2 in the hawthorn sere, is never more than occasional in the examples listed, but several other examples of scrub (hawthorn sere: Shirburn Hill, Pyrton Hill, Watlington Hill) contain locally abundant yew. Its occurrence and frequency are determined by the available protection from rabbits (**8**).

In general the progress of beech colonisation is slow, partly because of the remoteness of some examples (Lodge Hill) from seed-bearing trees, but partly because of the general scarcity of dense scrub which could act as a protection to the young trees. Where this protection is provided colonisation is free but never extensive.

The ash consocies.

Although ash has a high constancy in both seres it has a very low frequency and plays little part in the development of the vegetation on the escarpment. In the juniper sere the change from scrub to beechwood is effected without the frequency of the ash being appreciably altered; and this generally holds good for the hawthorn sere. As previously mentioned the rudiments of a consocies are found in the scrub at Wainhill, but as yet the community has no independent status.

On Aston Hill, however, an ash consocies showing various stages in the development from scrub to woodland is found. The ashes here occur as saplings and poles, the offspring of old trees whose stumps (local) are still recognisable. The oldest poles are about 60 years of age and 61 ft. (18·6 m.) high, with a diameter of about 6 in. (15 cm.) at 1 ft. (30 cm.) from the ground. The rate of diameter increase is slow: the first forty annual rings have an average width of 1·4 mm., the increase in stem diameter falling off rapidly in the outermost twenty rings, which average 0·5 mm. Some of the ash stems are straight, some are forked and some are badly cankered. Beech invaders of varying form are present and some of the larger have been cut.

The most frequent shrub is *Ligustrum*, but *Prunus spinosa*, *Rubus fruticosus* (agg.), *Sambucus* and *Viburnum lantana* have high frequencies locally. In the high frequency of *Prunus spinosa* we have evidence of the origin of part of the ashwood from scrub.

The mature ash consocies represented by one wood on the southern slope of a spur of Ashridge shows *Fraxinus dominant* 68 ft. (20·5 m.), *Quercus robur*

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[1] Both species of *Gymnosporangium* (*clavariaeforme* and *juniperinum*) are found on the escarpment, but whereas occasional *Crataegus* bushes may be severely attacked by *Roestelia lacerata*, *Roestelia cornuta* is not common on the occasional *Sorbus aucuparia*.

(o.-f.), *Fagus silvatica* and *Acer pseudoplatanus* occasional. The shrub layer reflects the development to maturity by the absence of typical scrub species, and by the presence of an open shrub layer of *Crataegus* (f.), *Corylus* (o.-f.), *Sambucus* (o.-l.a.), *Rubus fruticosus* (o.) and *Euonymus* (r.).

A comparison of the ground vegetation of the immature and mature ashwood brings out the same features noted from the corresponding beechwoods; and this is evident even although the immature wood includes relicts from grazed pasture (*Clinopodium vulgare*, *Hypericum hirsutum*) and accidentals (*Arctium*, *Epilobium parviflorum*) whose appearance is due to exposure of the mineral soil following the felling and removal of the beeches. *Mercurialis perennis* predominates in both and varies from 12 to 20 in. (30–51 cm.) in height. The development from immaturity to maturity consists essentially in the elimination of the rosette hemicryptophytes or species of low-growing form, as is shown by a comparison of the following lists of all the species with frequency higher than occasional.

		Immature ash consocies	Mature ash consocies
H.r.	Fragaria vesca	f.-a.	—
H.r.	Viola hirta	f.	—
H.r.	V. silvatica (agg.)	f.	—
H.s.	Geum urbanum	o.-f.	o.-f.
H.s.	Mercurialis perennis	a.-l.d.	d.
H.s.	Urtica dioica	l.d.	o.-l.a.
G.r.	Circaea lutetiana	f.	l.a.
G.r.	Asperula odorata	f.-a.	—

The predominance of hemicryptophytes with leafy flowering shoots establishes the affinity of the consocies with the hawthorn sere.

	Ch.	H.r.	H.s.	H.e.	G.r.	G.b.	T.	Total
Immature ash consocies (one example—all species of the ground flora)	2	5	12	5	2	1	2	29
Mature ash consocies (one example—all species of the ground flora)	3	2	7	3	2	1	1	19
Immature and mature ash consocies	3	6	12	7	3	1	2	34

This is supported by the presence of the chamaephytes (*Nepeta*, *Veronica chamaedrys* and *V. montana*), the absence of the rhizome-geophytes *Cephalanthera*, *Neottia* and *Helleborine* and of the saprophyte *Monotropa*—all typical of the sanicle beechwoods—and the elimination during development of the low-growing plants previously mentioned, together with *Bromus asper*, *Deschampsia caespitosa*, *Geranium robertianum* and *Primula vulgaris* (all occasional in the immature wood).

The most frequent mosses are *Brachythecium rutabulum*, *Eurhynchium praelongum* and *striatum*, *Fissidens taxifolius*, and in the immature wood *Hylocomium triquetrum*.

On the Chilterns there is no clear evidence that the protection from the prevailing south-west winds afforded by beech has an effect upon the survival of ash and the development of an ash community, though on Aston Hill the bulk of the ash has grown up between the beech pioneers. In parts there is direct invasion of *Prunus spinosa* scrub by ash, but in the remainder there is an absence of old ash stumps, and the scattered beech pioneers (including those felled) are much older than the accompanying ash. It therefore seems likely that the beech had invaded grassland or an open scrub and that the ash has grown up in the intervals between the trees of an open beech community. It is of interest to note that, a little to the east of the woodland described, ash saplings are growing freely on the old tracks leading up the hill and in the neighbourhood of a disused quarry.

Fragments of the ash consocies with *Mercurialis* dominant in the ground flora are met with in other places, for example, on the hill above Halton (also called Aston Hill) where trees of 77 ft. (23·4 m.) and 67 ft. (20·4 m.) were measured, the latter with a girth at breast height of 5 ft. 2½ in. (159 cm.).

The immature beech consociation.

Despite the severe rabbit pressure the beech is progressive, forming communities in all stages of development between scrub and grassland with a few trees and mature beechwood. The source of the invasion is generally the abundant woodlands on the plateau above, but occasionally in the beech plantations on the lower escarpment slopes. As these planted woods are scarce, beech generally is spreading down the slope. The rate of progress is slow: the distance between the nearest woodland with closed canopy and the beech pioneers in scrub is often less than 100 yards. Moreover much of the invasion appears to be relatively recent. This is particularly true of the juniper sere, in which the woodlands are young and small, with the beech in almost full occupation of the ground. In the hawthorn sere there is much greater variation: isolated beech pioneers occur, beech families and groups of various sizes and degrees of maturity. And the state of the subsidiary vegetation similarly varies: beech with dead scrub underneath, clumps of beech with a bare floor, a mixture of grassland and woodland species, a mixture of woodland species which have not yet entered into full competitive relations with each other, and finally local patches of vegetation characteristic of mature beechwood. The influence of these invading beeches extends into the enclaves of grassland or open scrub, and under lateral shade true woodland species (*Mercurialis perennis*) and wood edge species (*Nepeta glechoma*) replace the heliophilous species of grassland. In the juniper sere the transition from scrub and grassland to woodland is usually abrupt: in the hawthorn sere gradual, with developmental stages characterised by a mixed flora.

The structure of the immature beechwoods varies so much from place to place that the full significance of the floristic and vegetational details is thrown into relief only by considering them in relation to the scrub and grassland on the one hand and the mature beechwood on the other; and by a comparison of the different degrees of development shown within the immature woods of the hawthorn sere themselves. Hence a general account only is given here. This course is further to be recommended because of the unequal number of samples available for comparison: four from the juniper sere and thirteen from the hawthorn sere.

Apart from beech, which of course has increased in frequency (4·6 in the juniper sere; 4·3 in the hawthorn sere: constancy 5 in both) the other trees *Fraxinus excelsior*, *Sorbus aria* and *Ilex aquifolium* show no significant change. It is otherwise with the shrubs.

In enclaves the bulk of the scrub species survive with slight changes only in their constancy and average frequency, but under closer canopy some, like *Rosa dumetorum* and *R. eglanteria*, are eliminated, some (*Rubus fruticosus* (agg.), *Corylus avellana* and *Sambucus nigra*) maintain their values, others (*Rosa arvensis* and *Hedera helix*) show definite increases both in constancy and average frequency, whilst *Rubus idaeus* is the only species occurring in the immature beech consociation which is not recorded from scrub. The behaviour of juniper and hawthorn presents a marked contrast. As would be expected the light-loving juniper is quickly killed out in both seres by the beech. The hawthorn practically maintains its constancy in both seres but, while its average frequency is maintained in the juniper sere at its low value of 2·2, there is a significant drop from 3·7 to the same low value in the hawthorn sere. These values of high constancy and low average frequency are maintained in the mature woods of the juniper and hawthorn sere respectively.

Because of the unequal number of examples from which the lists were obtained, no deduction can be made from the difference in the number of species recorded from the field stratum (thirty-six in the juniper sere; ninety-eight in the hawthorn sere). The ninety-eight species include many ruderals and a few grassland species but also many species characteristic of the mercury wood. All the thirty-six are found in the immature mercury wood, except *Stachys silvatica*, which is local only. Moreover it occurs in the mature mercury wood. The significant species are given in the table on p. 254 and arranged in life form groups. Within each relevant group the species characteristic of the sanicle wood are placed at the beginning and those at the end characterise the mercury wood.

Detailed comparison between the spectra is not permissible, but the spectrum of the mercury wood (where the number of examples justifies comment) is lacking in "character"; no single life form is outstandingly predominant. The following observations are however warranted by the data. Few of the species have in these immature woods "declared themselves" definitely as belonging to one type or the other, and differences in constancy are sometimes offset by opposing differences in average frequency. Apart from those species not recorded from the immature sanicle wood—and the small number of examples scarcely justified the conclusion that these cannot grow

Species of the field stratum with high constancy and/or high average frequency.

		Immature sanicle wood		Immature mercury wood	
Life form		Constancy	Average frequency	Constancy	Average frequency
Ch.	Lamium galeobdolon	—	—	3	2·5
Ch.	Nepeta glechoma	—	—	2	3·0
H.r.	Sanicula europaea	5	2·5	2	2·5
H.r.	Viola silvatica (agg.)	4	2·2	5	2·5
H.r.	V. hirta	4	1·3	4	1·8
H.r.	Fragaria vesca	3	2·5	5	2·6
H.r.	Primula vulgaris	3	2·0	4	1·8
H.r.	Oxalis acetosella	(1) 2	l. 1·0	2	2·4
H.r.	Potentilla reptans	—	—	(2) 1	l. 2·5
H.s.	Lactuca muralis	4	2·0	3	2·0
H.s.	Epilobium montanum	3	2·0	4	2·1
H.s. (G.r.)	E. angustifolium	2	2·0	4	2·1
H.s.	Geum urbanum	3	2·0	5	2·1
H.s.	Urtica dioica	—	—	4	2·7
H.s.	Mercurialis perennis	(1) 2	l. 1·0	5	3·4
H.c.	Bromus asper	4	2·3	2	1·8
H.c.	Brachypodium silvaticum	4	2·3	5	2·0
H.c.	Deschampsia caespitosa	3	2·0	3	2·1
H.c.	Milium effusum	(1) 2	2·0	(2) 1	2·3
H.c.	Agrostis alba	—	—	2	2·2
H.c.	Hordeum silvaticum	—	—	1	2·5
G.r.	Cephalanthera grandiflora	5	2·0	2	2·0
G.r.	Helleborine latifolia	—	—	1	2·3
G.r.	Asperula odorata	3	2·5	4	2·4
G.r.	Circaea lutetiana	(1) 2	l. 2·0	3	2·1
G.b.	Arum maculatum	—	—	2	2·1
T.	Geranium robertianum	3	2·0	5	2·0
T.	Galium aparine	(1) 2	l. 2·0	4	2·2

Biological spectrum of species with high constancy and/or high average frequency.

	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	T.	Total
Immature sanicle wood	0	4	1	2	2	0	0	9
Immature mercury wood	2	7	5	5	4	1	2	26

there, for some species like *Monotropa hypopitys* and *Neottia nidus-avis* which are characteristic of the mature sanicle wood were not seen—only *Sanicula europaea*, *Bromus asper* and *Cephalanthera grandiflora* may at this stage be put down as characteristic of the juniper sere, whilst *Mercurialis perennis* and *Circaea lutetiana* may be selected definitely as species characteristic of the hawthorn sere. Thus the differences in life form which separate the mature woods of the two seres are already apparent. The rest of the species show slightly higher values in one sere or in the other and the degree to which they are characteristic of the respective seres cannot be finally decided until comparison is made with the mature woods. In short, the data given are an expression of a vegetation in which the competing life forms have not yet come to grips in the struggle for mastery. In the immature sanicle wood the potential dominant is sanicle. In the immature mercury wood, mercury has a constancy of 5 and an average frequency of 3·4—the highest value for any species—and, although unequally prevalent in the different examples as well as in one and the same example, it determines the physiognomy of this type.

Although there is much bare ground in the sanicle wood, there are only twenty-four bryophytes recorded against forty-one from the mercury wood, and in both the ground is only sparsely occupied by them. The frequencies of the less widely distributed species have not been completed, but *Brachythecium rutabulum*, *Eurhynchium striatum* and *Hypnum molluscum* have average frequencies ranging from 2·0 to 2·9 and a constancy of 4. Significant differences in constancy are not found in any, but *Dicranum scoparium* and *Madotheca platyphylla* have high local frequencies (average frequency 3·0) in the juniper and hawthorn sere respectively.

Quercus robur (constancy 2; average frequency 2·0 in the juniper sere: 2 and 1·8 in the hawthorn sere) plays no part in the succession. Young plants only were observed in the juniper sere, but in the hawthorn sere older examples are found. One with a free and unshaded crown measured 20 ft. (6·1 m.) with a basal diameter of about 1 ft. (30 cm.).

Although the constancy of *Fraxinus* (4 and 5) remains high the records do not show that the frequency of ash (2·0 and 2·2) is increased by the companionship of beech, nor is there a significant difference between the frequencies in the two seres. Only in one example have old ashes of pioneer form been seen, and the adjoining beeches looked equally old. But in the hawthorn sere groups of sapling ash, though local, are widespread and indicate the potentialities of the habitat. Small ash plants kept down by grazing are locally common in grassland enclaves, and in two areas where the beech is advancing up the escarpment, an incipient ash consocies in the form of a narrow border of young trees was observed along, or in patches on, the forward margin. Again the disturbed soil of old tracks is overgrown by a mixture of young ash and beech.

Carpinus appears to be a secondary species. It does not reach the canopy in any example, and it occurs either as boundary (and planted ?) trees or as young growth in the neighbourhood of them.

The beech consociation.

The abrupt transition from scrub and grassland to the immature beechwood of the juniper sere is followed almost directly by development to the mature consociation, in which only occasional elements of scrub and grassland linger near the margins. A good characterisation of these sanicle woods is got from fourteen examples, eight of which in the neighbourhood of Whiteleaf Hill are managed as "protection forest," thus ensuring continuity of cover and the maintenance of a typical woodland flora. In the hawthorn sere development is slower, and in parts the ground vegetation has not attained full maturity. Moreover only four out of the nine examples listed have continuous canopy, the other five woods having been partially and selectively felled, thus allowing ruderals to enter. But comparison with the unfelled woods shows that the essential character of the ground vegetation remains unaltered.

This approach to almost complete maturity is reflected in the same number (thirty-four) of woody species from each type—a number already nearly reached in the almost closed immature sanicle wood (thirty-one) but showing a slight drop from forty in the immature mercury wood.

The canopy is formed almost exclusively of *Fagus* with highest constancy in both seres and the highest average frequency in the sanicle wood, but (owing to felling) only 4·4 in the mercury wood. *Fraxinus* (constancy 5 in both) is found in practically every example, but has a relatively low average frequency (2·0 and 2·2 respectively). Besides the tall stems, young suppressed and small ash plants are fairly common in the sanicle wood, but not in typical examples of the mercury wood. The different heights attained by the beech in the two seres (67 and 77 ft.) probably accounts for the survival in the sanicle wood canopy of *Sorbus aria* (constancy 4; average frequency 2·0) and its relegation to the shrub layer in the mercury wood where it has a constancy of 2 only and an average frequency of 1·7. *Carpinus* does not occur and *Quercus robur* is represented in both seres by seedlings and young plants only.

The shrub layer is sparse; and only a few species have high constancy, and still fewer a high average frequency. *Rubus fruticosus* (agg.) and *Crataegus* have high constancies and relatively low average frequencies in both seres. With constancy 4 in the juniper sere and much lower values (in brackets) in the hawthorn sere we have *Cornus* (2), *Hedera* (2), *Rosa arvensis* (2) and *Viburnum lantana* (2). *Sambucus* (with 2 in the juniper sere) is the only shrub with the highest constancy in the hawthorn sere. *Hedera*, besides climbing trees, forms ground societies in the sanicle wood: in the mercury wood it is occasional only, its high average frequency being due to local dominance in one example where it is associated with locally dominant sanicle—a fragment of sanicle beechwood. All these woody species have fleshy fruits, and all except *Crataegus* and *Sambucus* have the power to reproduce vegetatively. How far the exclusion (e.g. of procumbent and low-growing *Viburnum opulus* and *Viburnum lantana*) and the reduced constancy and average frequency of the species mentioned is due to the tall dense growth of *Mercurialis* is not known, but low growing and suppressed shrubs would find difficulty in getting the light necessary for survival, and establishment by seed would generally be impossible.

The attainment of maturity brings about marked differences in the field stratum, revealed primarily in the number of species from each sere. In the sanicle wood the number has risen to eighty (thirty-six in the immature wood): in the mercury wood it has dropped to sixty-nine (ninety-eight in the immature wood). Further, in the sanicle wood the layer is not quite continuous, whilst mercury, in typical examples, forms dense masses. Hence the addition or exclusion of species and the readjustments in constancy and frequency of those already present bring about considerable changes; and because of these, the attainment of maturity accentuates and amplifies the differences already noted.

For convenience the species with high constancy and high average frequency are listed here in three groups: those with high values (1) in the sanicle wood, (2) in the mercury wood, and (3) in both types of woods. Some of the species with high values in both seres have been assigned to group (2) on the basis of a large difference in the average frequency values or after a careful scrutiny of their distribution in the examples of each type: "L." before the average frequency means that the species is exclusively local in one or more examples and an asterisk before the constancy figure means that the species is recorded from one example only. The figures in brackets are the corresponding values in the contrasted sere.

The species with constancy 4 and 5 include nearly all with high average frequency: only six out of the thirty-three listed combine high average frequency with a low constancy in one or other of the seres.

(1) *Species with high constancy and/or high frequency in the sanicle wood.*

Life form	Species	Constancy	Average frequency
H.r.	Sanicula europaea	5 (3)	4·3 (1·9)
G.r.	Asperula odorata	5 (3)	2·6 (1·4)
H.s.	Lactuca muralis	5 (2)	2·1 (2·0)
H.c.	Brachypodium silvaticum	5 (3)	2·1 (1·8)
H.c.	Bromus asper	4 (2)	2·2 (1·7)
H.c.	Deschampsia caespitosa	4 (2)	2·0 (1·7)
G.r.	Helleborine latifolia	4 (2)	2·1 (2·0)
G.r.	Cephalanthera grandiflora	4 (2)	2·1 (1·8)
G.r.	Neottia nidus-avis	4 (*1)	1·8 (L. 1·0)
G.rad.	Monotropa hypopitys	4 (2)	2·0 (1·5)
G.r.	Carex glauca	4 (–)	2·1 (–)
H.c.	Festuca rubra	4 (–)	2·1 (–)
H.s.	Campanula rotundifolia	4 (–)	1·8 (–)
T.	Geranium robertianum	2 (3)	2·2 (1·8)

(2) *Species with high constancy and/or high frequency in the mercury wood.*

Life form	Species	Constancy	Average frequency
H.s.	Mercurialis perennis	5 (5)	4·3 (2·3)
H.s.	Urtica dioica	5 (2)	2·9 (L. 3·3)
G.r.	Circaea lutetiana	5 (1)	2·2 (L. 2·0)
Ch.	Veronica chamaedrys	5 (3)	2·0 (1·7)
T.	Galium aparine	5 (*1)	1·8 (L. 2·0)
H.s.	Scrophularia nodosa	5 (2)	1·7 (1·7)
T.	Myosotis arvensis	4 (1)	1·8 (1·0)
H.s.-G.r.	Epilobium angustifolium	4 (2)	2·7 (L. 2·3)
H.s.	Ajuga reptans	4 (3)	1·8 (1·6)
H.s.	Geum urbanum	4 (3)	2·0 (1·9)
H.s.	Epilobium montanum	4 (3)	2·0 (1·9)
H.c.	Agrostis alba	2 (*1)	2·2 (L. 1·5)

(3) *Species with high constancy and/or high frequency in the sanicle and mercury wood.*

		Sanicle wood		Mercury wood	
Life form	Species	Constancy	Average frequency	Constancy	Average frequency
H.r.	Fragaria vesca	5	2·8	5	2·2
H.r.	Viola silvatica (agg.)	5	3·2	5	2·3
H.r.	V. hirta	5	1·7	4	1·7
H.s.	Senecio jacobaea	4	1·8	4	2·1
H.s.	Arctium minus	4	1·9	4	2·0
H.r.	Primula vulgaris	3	2·3	4	1·4
G.r.	Anemone nemorosa	2	2·8	2	2·5

The distinctive physiognomies of the two types are due to the high average frequency of *Sanicula* and *Mercurialis* in the respective seres. Mercury, however, has higher values (constancy 5; average frequency 2·3) in the sanicle wood than sanicle (constancy 3; average frequency 1·9) in the mercury wood. The other species show much smaller differences. If we neglect the species with high local frequency only, then the species of group (1) have slightly higher values in the sanicle wood and include *Asperula odorata* (local in most examples of the mercury wood) with a difference of 1·2; and the species of group (2) have slightly higher values in the mercury wood. In group (3) *Fragaria, Viola silvatica* and *Primula* (largely local in the mercury wood) have higher values in the sanicle wood with differences of 0·6, 0·9 and 0·9 respectively.

In the sanicle wood nineteen species have high constancy; in the mercury wood seventeen. In group (1) all the species except *Geranium robertianum* have significantly higher constancies in the sanicle wood; in group (2) all except *Mercurialis, Ajuga, Geum* and *Epilobium montanum* have significantly higher values in the mercury wood.

The significance of these data becomes clear from analysis of the life forms in the two seres.

	Ch.	H.r.	H.s.	H.c.	G.r.	G.rad.	T.	Totals
Sanicle wood								
From group (1)	0	1	2	4	5	1	1	14
From group (3)	0	4	2	0	1	0	0	7
Totals	0	5	4	4	6	1	1	21
Mercury wood								
From group (2)	1	0	7	1	2	0	2	13
From group (3)	0	4	2	0	1	0	0	7
Totals	1	4	9	1	3	0	2	20

The chief difference between these two spectra is the predominance of the hemicryptophyta scaposa in the mercury wood. Further, the lack of "character" or the approximate numerical equality between the subdivisions of the hemicryptophytes and the rhizome geophytes which is a feature of the *immature* mercury wood also characterises the *mature* sanicle wood, although the emphasis is shifted from the hemicryptophytes to the rhizome geophytes.

Species showing a low average frequency in the mercury wood and a high average frequency in the sanicle wood with a high or low constancy in either or both seres are particularly instructive. Good examples are the rosette plants *Primula vulgaris*, *Viola silvatica*, *Fragaria vesca*, the geophyte *Asperula odorata*, and less obviously the geophyte *Anemone nemorosa* and the winter green annual *Geranium robertianum*. Combinations of this kind mean that conditions allow of the species existing in both seres, but that only in the sanicle wood are they suitable for more than occasional occurrence. And this is true even although, as is well shown by the greater vigour of *Asperula* and *Geranium*, the mercury wood is the more favourable habitat.

The explanation of this combination of values as well as the key to the structure of the mercury wood spectrum is found in the dominance of tall growing *Mercurialis*. It has dark green leaves and over large patches forms dense masses (gregariousness 5) with an average shoot height of 15 in. (37·5 cm., extremes 9 in. and 20 in.: 22·5 and 51 cm.). In the sanicle wood, mercury is represented by isolated scattered non-flowering individuals (gregariousness 1) of low stature (average height about 6 in. = 15 cm.) growing larger in gaps and less dense woods. Now in the mercury wood and in two large patches where mercury is dominant, the following species only are found mixed with it: *Circaea lutetiana* (o.-f.), *Urtica dioica* (o.-l.d.), *Arctium minus* (o.), *Campanula trachelium* (o.), *Scrophularia nodosa* (o.), *Dryopteris filix-mas* (r.), *Lamium galeobdolon* (r.), *Asperula odorata* (l.), together with *Atropa belladonna*, *Bryonia dioica*, *Rubus idaeus* and *Solanum dulcamara*. On the other hand, wherever the mercury is not completely dominant owing to a slightly shallower soil or a slope steeper than in the type, or to exposure to sun and wind and disturbance following recent felling, some of the sanicle wood species attain a high frequency. Thus where mercury is 9–12 in. (22·5–30 cm.) and less dense (gregariousness 3) with paler green leaves than in the normal taller form, rosette plants and low growing geophytes occur with a high frequency—*Fragaria*, *Viola silvatica*, *Sanicula*, *Primula vulgaris*, *Asperula odorata* and *Anemone nemorosa*. It is this feature which robs the spectrum of the mercury wood of an outstanding predominance of hemicryptophytes with leafy flowering stems.

In view of these facts we may arrive at the spectrum of a typical adult mercury wood by assigning the following species of group (3) to the sanicle wood: *Fragaria vesca*, *Viola hirta*, *V. silvatica*, *Primula vulgaris* and *Anemone nemorosa*, leaving *Arctum minus* and *Senecio jacobaea* common to both types. The ruderal *Myosotis arvensis* may also be omitted from the typical Mercury spectrum. The spectrum of the sanicle wood remains as before: that of the mercury wood now becomes:

Ch.	H.r.	H.s.	H.c.	G.r.	T.	Total
1	0	9	1	2	1	14

This distribution of life forms and their numerical representation is approximately what is found in patches of dominant mercury, and emphasises the difficulties attending the establishment and growth of low-growing plants in the face of such a well-equipped opposition.

The attainment of maturity brings about considerable changes in the bryophytic layer, whose development is related to the thickness of the leaf litter and the nature of the herbaceous cover. In the sanicle wood, with relatively open field stratum and sparse leaf litter, the ground stratum is well developed, with forty-four species represented: in the mercury wood the thick leaf litter and typical dense herbaceous canopy preclude the good development of this layer which is, however, represented by thirty-eight species, most of which occur, some with a high frequency, where the layer of litter is thinner or the herbaceous canopy open.

Of the ten species with high constancy in the sanicle wood, and the six in the mercury wood, five (*Eurhynchium striatum*, *Hypnum molluscum*, *Brachythecium rutabulum*, *Hypnum cupressiforme*, *Mnium undulatum*) are common to both. Those not common show significant differences: *Plagiochila asplenioides* (constancy 5 in the sanicle wood, 2 in the mercury), *Anomodon viticulosus* (4 and 1), *Mnium hornum* and *Dicranum scoparium* (4 and 2) have higher values in the sanicle wood: *Fissidens taxifolius*, with constancy 5 in the mercury wood and 3 in the sanicle wood, is the only one with a significantly higher value in the hawthorn sere.

The records of frequency are incomplete, but seven in the sanicle wood and eight in the mercury wood have values of 2·1 and over. *Eurhynchium striatum*, *Hypnum cupressiforme* and *H. molluscum* are common to both: *Plagiochila*, *Madotheca*, *Eurhynchium myosuroides* and *Dicranum* in the juniper sere, and *Brachythecium purum*, *B. rutabulum*, *Fissidens*, *Eurhynchium praelongum* and *E. schwartzii* in the hawthorn sere, have high values, but they are not significantly different except in the case of *Hypnum molluscum* (3·5 in the sanicle wood; 2·6 in the mercury wood) which sometimes forms continuous carpets on steep slopes in the sanicle wood.

The beech trees are uneven aged, but by far the larger number belong to the larger diameter classes, with a few individuals only of smaller size. In practice it amounts to an even-aged wood. In the sanicle wood mature trees average 67 ft. (20·5 m.) (extremes 54 and 77 ft.); in the hawthorn sere 77 ft. (23·5 m.) (extremes 70 and 85 ft.). Their age is approximately 120 (±20) years.

In some examples of the mercury wood felling has been carried out either of single trees, groups of trees, or of the whole crop with the exception of scattered trees intended perhaps to serve as seed bearers for restocking the ground. The regeneration is not in fact very successful, owing to rabbit attack, but in one wood groups of sapling beech are common, whilst in the sanicle wood young beeches of the 1922 mast year are locally abundant—although they have decreased rapidly in number in the succeeding years. Again in the sanicle wood ash seedlings, small but several years old, and groups of saplings are occasional, whilst groups of saplings are frequent in gaps in the mercury wood. Here the annual shoots may be 2 ft. (61 cm.) or more in length and the bark of the older parts of the stems is green and lush, contrasting with the drier looking, whitish-grey bark of saplings in the sanicle woods. In the mercury woods groups of sapling sycamore are occasionally found and seedling oaks and small oaks a few years old occur occasionally in both types.

In none of the examples is there a distinct shrub layer, but in a beechwood (hawthorn sere) above Halton an example is found where *Taxus baccata* and *Buxus sempervirens* form the undergrowth of a two-layered community, for neither herbs nor mosses exist below the dense canopy and on a litter covered soil.

The structure of the beech root system is largely determined by the soil. In the sanicle woods the numerous ramifications of fine roots form a compact network, with a concentration of stronger roots running horizontally near the surface. In some root systems this network is apparently limited to the surface weathered soil (9–15 in.; 22·5–37·5 cm.), but in one example an upturned tree showed two distinct regions, an upper zone of "feeding" roots and a lower of vertically and obliquely descending "anchoring" roots of relatively small size penetrating the compact chalk to a measured depth of 43 in. (109 cm.) and probably extending *in situ* to 48 in. (122 cm.). In the mercury woods the root system shows a similar concentration of stronger roots running horizontally in the upper soil layers, but the zone of feeding roots extends deeper to the unweathered chalk (at 20 in.; 50 cm.) or forms a diffuse system in the relatively soft chalk penetrating at least 36 in. (91 cm.), but in all probability much deeper.

The root systems of the herbs have not been studied, but Salisbury (**5**) gives the average depths of sanicle and mercury roots as 4 in. (10 cm.) and 3–4 in. (7·5–10 cm.) respectively. While sanicle is entirely fibrous-rooted mercury has rhizomes which run just in the surface soil layer or sometimes upon it, protected in the latter case by a layer of leaf litter.

COMPARISON AND DISCUSSION OF THE SPECTRA OF THE SIGNIFICANT SPECIES OF THE FIELD STRATUM OF THE IMMATURE AND MATURE SANICLE AND MERCURY WOODS.

In passing from the immature to the mature wood the number of species of the field layer with high constancy shows an increase in both seres: from 7 in the immature to 19 in the mature sanicle wood and from 13 in the immature to 17 in the mature mercury wood. On the other hand, while the number of species with high frequency increases in the sanicle woods from 6 to 17, there is a big drop in the mercury woods from 21 to 9. Further, because the examples of the immature sanicle wood are in an early stage of development, no species with high constancy and/or high average frequency in the immature wood drops out in the climax beechwood. In the mercury woods there is a net loss of 8. This figure is arrived at as follows: there is an increase of 7 with high constancy, but a loss of 3 (result +4): on the other hand there is an increase of 2 with high average frequency but a loss of 14 (result −12).

Gains and losses in life forms during the change from immaturity to maturity in the sanicle and mercury beechwoods.

	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	G.rad.	T.	Total gain or loss
Juniper sere	0	+1	+6	+2	+5	0	+1	+1	+16
Hawthorn sere	−2	−3	0	−4	−2	−1	0	−1	−13
	+1	0	+4	0	+1	0	0	+1	+ 7
	−1	−3	+4	−4	−1	−1	0	0	− 6

The distribution of the life forms of species which, because of changes in their constancy and/or average frequency, are included or removed from the list of significant species brings out an important difference between the two seres during development (data on pp. 241 and 242). In the juniper sere (with gains only) the addition of the saprophyte *Monotropa* and the therophyte *Geranium* extends the range of the spectrum, while the existing classes are augmented with maximum increases in the hemicryptophyta scaposa and the geophyta rhizomata. By contrast the readjustments in the mercury wood lead to a reduction in the number of all life forms except the therophytes and the hemicryptophyta scaposa: the latter show an increase of 4.

The key to the changes during development of the mercury wood is found in the life form of *Mercurialis perennis*. It is an early leafing and early flowering plant; it has tall erect shoots with marked leaf mosaic; it is highly social, spreading freely by rhizomes; and its leaves persist well into the winter. Against this life form only those with similar equipment prevail. If we bear in mind that the mercury woods examined have been much disturbed and are not uniformly typical, we may conclude generally that in the *ideal* or *type* example all life forms are excluded by dominant mercury except the hemicryptophyta scaposa or plants with similar shoot form and the scrambling winter green therophyte, *Galium aparine.* And in the woods as they are, species of the other life forms which retain a high constancy and/or high average frequency in the mature mercury wood generally show a reduction from the values in the immature wood; whilst the same species in the development of the sanicle wood generally show an increase or retain similar values.

For the elimination or numerical reduction of all short-stemmed or low-growing plants, the exclusion of light by a canopy of tall mercury seems to afford an adequate explanation. Thus the chamaephytes *Lamium galeobdolon, Nepeta glechoma,* the rosette hemicryptophytes *Fragaria vesca, Viola silvestris, V. hirta, Primula vulgaris, Oxalis acetosella, Sanicula europaea, Potentilla reptans, Taraxacum officinale,* the rhizome geophytes *Asperula odorata, Carex glauca* and *Campanula rotundifolia* among hemicryptophytes with leafy flowering stems, are or tend to be excluded from the mercury wood and, with the rhizome geophyte *Anemone nemorosa,* have on the whole increasing values in the sanicle wood. On the other hand tall plants, whether hemicryptophytes with rosettes (*Dryopteris filix-mas*) or with leafy stems (*Arctium minus, Senecio jacobaea, Urtica dioica, Epilobium angustifolium, E. montanum, Geum* *urbanum*, *Scrophularia nodosa*, *Ajuga reptans*), or the rhizome geophyte *Circaea lutetiana* persist in competition with mercury, retaining approximately the same values, some showing a slight decrease but most showing an increase.

The exclusion of light may also account for the behaviour of the grasses and the biennial *Lactuca muralis* because the establishment of seedlings would be rendered difficult or impossible. With the exception of *Agrostis alba*, which maintains its values in the mercury wood, the grasses *Bromus asper*, *Festuca rubra*, *Brachypodium silvaticum*, *Deschampsia caespitosa* and *Hordeum silvaticum* have decreasing values in the mercury woods and increasing or similar values in the sanicle woods.

This explanation does not seem adequate to account for the similar behaviour of the geophytes, *Cephalanthera grandiflora*, *Helleborine latifolia*, and especially the saprophytic geophytes *Neottia nidus-avis* and *Monotropa hypopitys*; some more subtle competitive quality seems necessary to explain their reduced values in, or their elimination from the mature mercury wood. Despite high seed production and the association with or dependence upon root fungi, the competitive powers of these seem weak compared with mercury.

In the sanicle wood the field stratum is not continuous, and therefore not closed against invasion. Hemicryptophytes with leafy stems, *Arctium*, *Senecio*, *Mercurialis* and *Campanula*, do in fact occur with a high constancy but a low frequency. Thus they do not seriously compete with plants of low-growing habit.

Now since all the species with high constancy and/or high frequency found in one sere do grow in the other, the habitat of the one is not exclusive to the species of the other. But it is equally clear that many species show a distinct preference: as a group the species with leafy flowering shoots grow much better in the mercury woods. But many species which are characteristic of the sanicle wood may and very likely do find the conditions of the mercury wood actually better for growth—at any rate they flourish in the immature mercury wood, where as yet they have not come to grips with mercury in the struggle for mastery. Their exclusion is therefore not due to habitat unsuitability but to an inability to hold their own with mercury.

The conclusion reached therefore is that the species characteristic of the mercury wood find the habitat conditions in the sanicle wood less than optimal; that the species characteristic of the sanicle wood are so, not necessarily by choice, but because they *can* grow in a habitat where competition with aggressive species like *Mercuralis* is excluded.

Interpretation of results.

The general course of the succession is the same in both seres. Grassland is replaced by scrub, and only the few scrub elements which can bear the shade of beech survive to make a very sparse shrub layer. The species of grassland are killed out by scrub or by beechwood, where they are replaced by woodland herbs which gradually cover the ground as the consociation attains maturity.

The two seres recognised are so closely related that the same species are found in both, and the different physiognomies reflect the discriminating effect of the habitat in the competition between the species. What has been said about the relation of sanicle to mercury in the beechwoods may be applied to scrub where juniper bears much the same relation to hawthorn as sanicle to mercury. Under the existing conditions of grazing, however, the dominance of *Crataegus* in hawthorn scrub is incomplete, and heavy grazing may so far discriminate in favour of the more resistant juniper that in some places it replaces hawthorn in the hawthorn sere. Here juniper becomes a much larger plant, although it shows unhealthy symptoms. The unpalatability of the woodland herbs prevents modification of the ground vegetation due to grazing.

The biotic factor does undoubtedly affect the rate of progress in succession. Scrub invaders of grassland may be so intensively grazed that full ecesis is difficult or impossible, and the invasion by beech or ash may, in the absence of protecting scrub, prove abortive, as also may regeneration within the beechwood. The biotic factor does not, however, exercise such a levelling effect that differences between the two seres in the successful establishment of trees are obliterated.

From the greater resistance of juniper to rabbit attack and the greater density of the juniper scrub, implying fuller protection to invading trees, a more active colonisation by ash and beech might be expected in the juniper than in the hawthorn sere. This is found not to be the case. For although the spread of beech is not very rapid in either sere, it is more active in the hawthorn sere. In the juniper sere the rarity of a general and progressive colonisation, resulting in abrupt transitions from grassland to scrub or beechwood, contrasted with the gradual change, and the production of more extensive immature beechwoods in the hawthorn sere, point to conditions more uniformly favourable for ecesis in the latter. Further, the ash as a wood-former is confined to the hawthorn sere, but even here the trees are relatively slow in growth, and the wide prevalence of forking (death of terminal buds or leading shoots) both in the juniper and hawthorn seres denote a hostile influence of widespread application (4). Protection from grazing animals, therefore, whilst conferring obvious advantages, does not fully explain the observed phenomena. The habitat of the hawthorn sere is more favourable to the successful establishment of ash and beech than that of the juniper sere.

Besides the biotic factor there is therefore another or others tending to retard the succession to woodland and preventing the development of a normal ash consocies. This factor is believed to be drought acting during the spring and militating against the establishment of woody plants, but relatively more hostile to the shallow rooting ash seedling than to the deeper rooting beech, and to the tropophilous hawthorn than to the xerophilous juniper. Further, in later life the more drought-resisting beech is more successful than the more mesophilous ash.

This factor tends to emphasise the difference between the two seres, determined primarily by soil depth acting through the soil water content, which is more eustatic in the hawthorn than in the juniper sere. The shallow soil of the juniper sere often found on steep and exposed slopes bears a more xerophilous vegetation and a less luxuriant growth of mesophytes common to both seres. But the basis of exclusion of the characteristic species is different: from the juniper sere, the species characteristic of the hawthorn sere are excluded or grow badly on physical grounds: from the hawthorn sere, those characteristic of the juniper sere are or tend to be excluded through competition.

Besides the evidence from the establishment of woody plants and the rate of progress of the succession, the following considerations support the conclusion that the physical habitat of the hawthorn sere (primarily its moisture relations) is more favourable to plant growth.

1. The total number of species in the hawthorn sere is higher. This is due chiefly to the larger number of herbs.

2. Among the species confined to the hawthorn sere, *Dryopteris filix-mas*, *Ranunculus repens*, *Arrhenatherum elatius*, and *Poa trivialis* are significant in this connection. On the Chilterns ferns are scarce both in species and individuals and on the escarpment the absence of *Dryopteris* from the sanicle woods is held to denote dryness. *Ranunculus repens* is a well-known damp-loving species. In the Cevennes Arrhenatheretum "is an enclave of the northern type in the Mediterranean vegetation explained by the abundant humidity and freshness of the habitat" (**3**), and in the Paris Basin Allorge refers the Arrhenatheretum to mesophilous grassland, where its ecological optimum is realised on calcareous or marly, well drained, but always fresh soil. *Arrhenatherum* also competes with *Bromus erectus* on dry calcareous soil but is absent from typical grassland of *Festuca duriuscula* (*F. rubra* var.) and *Sesleria coerulea* (**2**). Stapledon considers *Arrhenatherum* as a shade grass of dry places (**6**). *Poa trivialis* is essentially a meadow grass, sensitive to drought (**6**).

3. The significant species of the mercury wood include many which are well known to show a preference for a moist habitat, for example, *Ajuga reptans*, *Circaea lutetiana*, *Geum urbanum*, *Nepeta glechoma*, *Urtica dioica*. These also occur in the sanicle wood but with low constancy and low frequency and often local.

The relative drought resistance of *Sanicula* and *Mercurialis* has not been the subject of experiment, but Salisbury records *Sanicula* (and *Fragaria*) as particularly met with where the soil above the chalk is shallow: and Adamson states that on the north escarpment of the South Downs, mercury wilted after the long drought of 1911. No reference is made to sanicle, growing with or near it, and presumably no unusual behaviour attracted Adamson's attention.

In view of the dominance of hemicryptophyta scaposa in the mercury woods no deductions regarding habitat factors can be made from the absence, reduced frequency and constancy of those species characteristic of the sanicle woods. This is particularly true of the bryophytes, which occupy a much more important place in the sanicle woods (many of them living there because of their xerophytic adaptations (**9**)) than in the mercury woods, where heavy shade of beech and mercury prevents their active growth and spread.

4. The hemicryptophyta scaposa, which characterise the spectrum of the significant herbs in the mercury wood, have a more mesophytic organisation than the rosette hemicryptophytes and rhizome geophytes which characterise the spectrum of the sanicle wood.

5. The differences in height of some species common to both seres (*Fagus*, *Fraxinus*, *Crataegus*, *Juniperus*, *Mercurialis*) show that for them, and in all probability for the majority, the habitat of the hawthorn sere is more favourable to growth.

6. In particular ash is a plant sensitive to differences in atmospheric and soil moisture and its formation of an ash consocies in the hawthorn sere is strong evidence for the belief that the moisture conditions are more favourable in that sere.

7. The higher and more eustatic water content in a soil of this kind is more favourable to the activities of nitrifying organisms, and the greater frequency of *Fraxinus*, *Sambucus*, *Epilobium angustifolium*, *Geum*, *Urtica* and *Mercurialis* bear this out.

The vegetation of the escarpment is therefore found to be explicable in terms of the natural process of invasion and competition, and separable into two seres whose vegetation is the expression of the interaction of the habitat and the life forms of the dominant species.

COMPARISON WITH SIMILAR VEGETATION IN OTHER AREAS.

The affinities of the vegetation on the escarpment of the Chilterns and on similar areas of the South Downs, Cotswolds, Paris Basin, etc., are substantiated on a vegetational analysis in respect of the general succession and the floristic cortège of the beechwoods. The lack of full data from each area prevents a detailed comparison, but the existing information may be brought together and an effort made to harmonise the corresponding stages of the succession and to compare the biological spectra of the climax beechwoods.

The succession.

Cotswolds. In 1912 Tansley and Adamson (**7**) carried out a reconnaissance of the Central and Southern Cotswolds and concluded that on the Inferior Oolite escarpment and valleys of the Southern and Central Cotswolds the succession includes oolite pasture (equivalent to chalk grassland), ashwood and beechwood. In the beechwoods, *Sanicula* is recorded as abundant and *Mercurialis* locally abundant, but in "Witcombe wood, on the escarpment slope below Buckholt wood," ash is partly dominant with mercury generally dominant on the ground. Boxwood, regularly coppiced, occurs in one place in this habitat, where it has been present for several centuries, though there is no evidence as to whether it is native or originally planted.

South Downs. A fuller account of the beechwoods on the escarpment and valley slopes of the Western Downs is given by Adamson (**1**) who, in his summary, distinguishes two varieties: (1) beechwoods on the west-facing (and exposed) slopes of Middle Chalk with *Sanicula* the most abundant shade plant, and (2) beechwoods on the north-facing Lower Chalk escarpment with a ground flora largely composed of *Mercurialis perennis*. The following notes may be added to show that, while Adamson's separation is generally sound, some of the woods are really made up of the two varieties, one or the other covering a larger area and hence determining the character of the wood as a whole.

In the exposed west-facing wood of Oakham Bottom (Ditcham Park) *Sanicula*, *Viola silvestris*, *Ajuga reptans* and *Euphorbia amygdaloides* are generally spread, and *Mercurialis* occurs only in the lower part of the wood. Similarly in Wolver Wood (also exposed) *Sanicula* is the most frequent plant (abundant), but mercury is more abundant here than in Oakham Bottom. The soil however is rather deeper.

On the north-facing and sheltered escarpment, *Mercurialis* is generally dominant with *Sanicula* confined to the uppermost slopes of "the Miscombe." In Old Ditcham Wood, mercury is generally dominant with sanicle listed as frequent.

There is evidence here to show that *Sanicula* dominates in the more exposed and drier parts of these woods and *Mercurialis* in the more sheltered parts. There is apparently no direct correlation between the distribution of these two species and soil depth, e.g. mercury is found dominant on a soil of 9 in. (23 cm.) (sheltered).

The moisture relations of these two species seem to be important and in this area the relatively high rainfall (about 40 in.--1016 mm.) and proximity to the sea compensate the general dryness of a shallow soil on a steep but sheltered slope. In such areas *Mercurialis* dominates and only on the upper parts of the slopes where the evaporation rate is higher is *Sanicula* dominant.

This separation based on evaporation corresponds with that on the Chilterns determined by differences in soil moisture, and affords an excellent illustration of the influence of local climate and of how an atmospheric may compensate an edaphic factor. These shallow soils of the South Downs (exposed and sheltered) would in the drier atmosphere of the Chilterns support a sanicle beechwood. The substitution however does not appear to be complete, for *Sanicula* still has a fairly high frequency on the sheltered escarpment of the South Downs, and here the dominance of mercury is not so complete as to exclude it. Further, during very dry summers mercury may wilt. Nevertheless the tendency towards mercury or sanicle is quite definite.

While the beechwoods of exposed chalk slopes on the South Downs have not been investigated by me we may suppose that sanicle beechwoods terminate a sere beginning with chalk grassland and passing through juniper and chalk scrub. Ash in this sere does not form independent woods but comes in only under the protection of the beech as "secondary and dependent." The beechwoods of sheltered chalk slopes, on the other hand, terminate the full succession —chalk grassland, hawthorn scrub, ashwood, beechwood (mercury). No boxwoods occur on the South Downs but that on Box Hill in Surrey grows on the steep (south-facing) escarpment of the North Downs.

Paris Basin. Owing to human activity the primeval woodlands of the French Vexin have been largely destroyed, and Allorge, in his treatment of their modern representatives, groups together woodlands which under an "apparently uniform physiognomy hide an often considerable sociological complexity." Hence the seres are not easily disentangled. One sere, however, is clearly outlined:

Grassland (*Festuca duriuscula* and *Sesleria coerulea*) → juniper scrub → *Quercus sessiliflora* ± *Q. pubescens* (climatic climax).

Parts of other seres are recognisable but any attempt to link them up would convey a false impression of definiteness where none is given in the original.

Cevennes. On permeable calcareous soils at an elevation of 500–1000 m. a sere is described by Braun (**3**): grassland (Brachypodietum, *B. ramosum*), scrub (*Prunus spinosa*, roses, brambles) and a climatic climax of *Quercus sessiliflora* (including *Q. pubescens*). This Brachypodietum is the subseral grassland corresponding to the seral Xero-Brometum erecti.

Boxwood in this district is derived from these climax oakwoods, in which it forms an important constituent of the shrub layer.

It is considered that the successions as briefly summarised here form a graduated series in which the climax woodlands in particular express significant climatic differences. The successions corresponding to the juniper sere of the Chilterns are summarised below.

Locality	Grassland	Scrub	Climax woodland
Cevennes	Xero-Brometum erecti Subseral Brachypodietum	*Prunus spinosa*, etc.	*Quercus sessiliflora*, incl. *Q. pubescens*)
Vexin	*Festuca duriuscula*, *Sesleria coerulea*	Juniper	Ditto
Chilterns	*Festuca [illegible]ubra*	Juniper	Beechwood
South Downs (exposed)	*Festuca [illegible]ina*	Juniper	Beechwood

General comparisons.

The grassland of the juniper sere (Chilterns) is regarded as having affinities with the corresponding community of the Paris Basin. The scrub is similar in three of the areas and beechwood in our climate replaces oakwoods in similar areas in France.

Between the Chilterns and the South Downs we have, however, differences in size of the mature beeches. No measurements of height are given by

Adamson, but from personal observation the trees on the slopes of Oakham Bottom are much taller than the beech of the sanicle woods of the Chilterns. They are also much thicker: the average girth of 12 trees is 4 ft. 2 in. (127 cm.) (Oakham Bottom) and 4 ft. 9 in. (145 cm.) (Wolver Wood): on the Chilterns the corresponding figure is 3 ft. 6 in. (107 cm.). The habitat of the juniper sere is therefore less favourable to the growth of beech than that of the corresponding sere on the South Downs, and this unfavourableness is considered to indicate an approach to continental conditions which, in France, prevent beech succeeding oakwood of *Quercus sessiliflora* and *Q. pubescens*.

Our information concerning the seres corresponding to the hawthorn sere is more fragmentary, and where identification is doubtful all reference is omitted. The grasslands of the South Downs have a biological spectrum closely parallel to the Arrhenatheretum of Braun and Allorge and the relationship is strengthened by the physiognomic resemblances of some of the examples from the Central and Eastern Downs where grazing is not very severe.

Locality	Ch.	H.	G.	T.
Cevennes (irrigated)				
Atlantic Slope	4·5	79·5	7·0	9·0
Mediterranean Slope	4	72	6	18
Vexin	3	70	9	18
South Downs	5	72	10	13

In all probability the grassland of the hawthorn sere belongs here.

On the South Downs ashwoods and derivative calcicolous coppice contrast sharply with their absence or hesitant attempts to form woods on the Chiltern escarpment.

The beech is again much thicker from the South Downs, with an average girth of 6 ft. 8 in. (203 cm.) (at top of slope 5 ft. 10 in.—178 cm.) compared with 4 ft. 4 in. (132 cm.) on the Chilterns. Height measurements from the South Downs are not available.

The close relationship of the vegetation of these different areas is strengthened by the occurrence of boxwoods which, on the Chilterns, are found in the habitats of both the juniper and hawthorn sere.

Biological spectra.

Comparison of the biological spectra of the English beechwoods on the South Downs, Cotswolds and Chilterns shows a striking similarity, and reinforces the conclusions already reached regarding the essential conformity of the escarpment wood in all three areas.

	P.	Ch.	H.	G.	T.	Total
South Downs (Beechwoods on Chalk)	23 (28)	6 (7)	50·5 (62)	15·5 (19)	5 (6)	100 (122)
Cotswolds	23 (24)	8·5 (9)	47·5 (50)	18·1 (19)	3 (3)	100 (105)
Chilterns (Juniper and hawthorn seres)	25 (41)	7 (12)	52 (87)	12 (20)	4 (7)	100 (167)
Chilterns						
Juniper sere	27·5 (34)	7·5 (9)	48 (60)	13 (16)	4 (5)	100 (124)
Hawthorn sere	26 (40)	6·5 (10)	51·5 (79)	11·5 (18)	4·5 (7)	100 (154)

Detailed comparison cannot be made, because the number of examples from the South Downs is small (**1**) and the list from the Cotswolds (**7**) is the result of a reconnaissance only. But in the ground flora forty-nine species—and these include all the most important—are common to the three areas and a further thirty grow in two out of the three. These seventy-nine species yield a spectrum which is practically identical with that for the significant species of the beechwoods belonging to the juniper and hawthorn seres taken together.

Biological spectrum of forty-nine herbs and grasses common to the escarpment beechwoods of the South Downs, Chilterns and Cotswolds, together with thirty found in two out of the three.

Ch.	H.r.	H.s.	H.c.	G.r.	G.rad.	G.b.	T.	Total
8·5 (7)	16 (13)	36 (29)	13·5 (11)	17 (14)	1 (1)	4 (3)	4 (3)	100 (81)
		65·5 (53)			22 (18)			

Biological spectrum of the significant species (52) *in the sanicle and mercury beechwoods of the Chilterns.*

Ch.	H.r.	H.s.	H.c.	G.r.	G.rad.	G.b.	T.	Total
8·0 (4)	17 (9)	30·5 (16)	17 (9)	15·5 (8)	4 (2)	2 (1)	6 (3)	100 (52)
		64·5 (34)			21·5 (11)			

This spectrum may, until further work is done on the beechwoods of the Cotswolds and South Downs, be accepted as characterising English chalk beechwoods (*Fagetum calcicolum*).

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THE RELATION OF LEAF SIZE TO ROOT STRUCTURE IN *TRIFOLIUM REPENS*

By G. H. BATES.

(*With Plates XXIII and XXIV.*)

I. Mechanical influences upon root structure and leaf size.

In any observational studies of grassland communities the variation in the leaf size of *Trifolium repens* in different situations is very striking. The relation between this phenomenon and habitat is clearly apparent and is therefore of interest from the ecological point of view. The economic value of *T. repens* needs no emphasis: this species is the criterion of good pasture in the eyes of the grazier, and any factor affecting its productivity or competitive powers demands attention.

It is well known that leaf size is one of the distinctions between ecotypes of this species, but that the characteristic is not purely genetic is obvious from the fact that a change of habitat produces a change in leaf size in the same ecotype. If two ecotypes, distinguished by a different leaf size, are removed to a fresh habitat, the increase or decrease in leaf size induced upon them by the new habitat is, to a large extent, of the same proportion in both cases.

Observation shows very clearly that close cutting or grazing reduces leaf size, this being very noticeable in the case of lawns, where mowing is frequent, or on sheep walks in the regions of closest grazing. The same result is produced by treading, the effect of which is to remove leaves by damage, and thus act in much the same way as cutting or grazing, and in addition to consolidate the soil surface.

It is noticeable also that when runners proliferate from a dense colony of *T. repens* to an unoccupied area of ground and there establish fresh shoots, the leaves of these shoots are of greater size than those on the centre of the colony. This latter phenomenon may even be observed when a runner establishes a shoot upon a denuded worm cast in an otherwise dense turf.

It is a fact now generally accepted that the effect of denudation of foliage is to reduce the size and extent of the root system (**1**). The result is produced by the restriction of photosynthesis and the consequently reduced food supply to the underground organs. It is obvious that a restricted root range will entail a limited water supply, and it is reasonable to assume that this deficiency may result in an automatic diminution of leaf size. This will explain the observations described above.

Experiments.

To investigate the problem of leaf size in relation to root system, a series of four experiments was conducted in the years 1929–32, the same results being recorded in each instance. The work was carried out in the following manner:

In each case a garden soil was utilised, in the first two instances a heavy loam (Chesterfield, Derbyshire), and in the last two, a light loam (King's Lynn, Norfolk). In both cases the soil was neutral in reaction as the result of frequent liming.

Ten strips of *T. repens*, each 1 m. long, and containing the same quantity of seed, from the same source, were sown each year. The ten strips represented five treatments, each in duplicate, the position of each strip being randomised. It was thought that the above arrangement, and the fact that the trial was conducted four times in four different years, would obviate the possibility of soil or seasonal differences.

The treatments chosen were as follows:

Strips 1 *and* 1 *a* (control). Strips sown and left undisturbed throughout the season.

Strips 2 *and* 2 *a*. In this case the seeds were sown in normally loose soil and allowed to become established as seedlings. The soil was then consolidated by treading, care being taken not to injure the seedlings. After consolidation the plants were allowed to grow undisturbed.

Strips 3 *and* 3 *a*. Trodden and bruised by the foot at weekly intervals, commencing two months after sowing.

Strips 4 *and* 4 *a*. Cut at weekly intervals commencing two months after sowing.

Strips 5 *and* 5 *a*. These were laid down in the following manner. Containers were constructed from sheets of perforated zinc, each being 1 m. long by 10 cm. wide and 10 cm. deep. The containers were fitted with handles, filled with soil, and embedded in the earth. The seed was sown down the middle line of the container, in the same manner as with the other strips. Eight weeks after sowing the plants were lifted in the containers at weekly intervals, and any roots which had emerged through the perforations in the zinc (usually a large crop) were shaved off. The containers were then replaced in the soil. In this manner root range was directly restricted without interference with the foliage.

Results.

In each year the following results were obtained:

Strips 1 *and* 1 *a* (control). The growth was luxuriant and the leaves of large size. Had these plants been casually observed in the field they would have been regarded as "commercial" white clover and not as "wild" white clover. The root system was well developed.

Strips 2 *and* 2 *a* (consolidated soil). No difference was noted in comparison with the control as regards leaf size.

The root system was as well developed as in the case of the control, except that there was no growth of secondary roots in the first 2 cm. depth of soil. It was also noticeable that the runners did not establish roots as freely as in the case of the control, where the surface soil was loose.

Strips 3 *and* 3 *a* (trodden). The results were similar to those obtained by cutting, but the reduction in leaf size was not quite so great. This is accounted for by the fact that treading and partial injury of the leaf does not reduce photosynthesis so extensively as the removal of the entire leaf by cutting. Root range was again restricted, but it was impossible to give any measured comparison with the root range of the cut plants.

Strips 4 *and* 4 *a* (cut at intervals). Great reduction of leaf size was shown in comparison with the control. The number of plants did not diminish, nor was there any significant difference in the number of leaves. Root range was restricted.

Strips 5 *and* 5 *a* (root pruned only). A great reduction in leaf size was effected, comparable with that noted in the case of the strips which were cut at intervals. The root range was obviously restricted, but the pruning produced a comparatively dense growth of secondaries. The number of leaves was less than in the case of the cut plants (strips 4 and 4 *a*) and the difference appeared to be significant.

Observations showed the same result in each year. In 1932 it was decided to obtain a definite measure of comparative leaf size. This was carried out in the following manner:

Leaves were cut in bunches, at the ground-level, from each of the strips. The cuts from each were placed in separate receptacles and later the produce of each strip was mixed with that of the duplicate. From the five receptacles 100 leaves were picked in succession from each of them, thus giving 100 leaves from each treatment. The leaf area was measured by placing upon graph paper, tracing round the margin, and counting the number of squares covered by each leaf (1 leaf = 3 leaflets). The orthodox method was adopted, i.e. less than half a square was neglected, more than half a square was counted as one square. The results of these measurements are set out in Table I below.

Table I.

Strips	Treatment	Average area of leaves sq. mm.	Range of leaf area sq. mm.	Average area expressed as %
1 and 1 *a*	Undisturbed (control)	627	75–1260	100·0
2 and 2 *a*	Consolidated soil	603	68–1184	96·1
3 and 3 *a*	Trodden weekly	409	75– 910	65·2
4 and 4 *a*	Cut weekly	263	62– 734	41·9
5 and 5 *a*	Root pruned	244	60– 750	38·9

The establishment of shoots from runners made the identification of individual plants difficult, and as estimations would have been inaccurate in consequence they were not carried out. Increase of individuals by runner establishment may have been greater in some cases than in others; but in no case did a treatment reduce the original number of individuals.

Discussion of results.

Taking the strips 1 and 1 *a*, which were grown in a normally loose soil and left undisturbed throughout growth, as a control or standard, it will be noted that the other treatments had a marked effect upon leaf size.

In the case of strips 2 and 2 *a* the reduction of leaf size cannot be regarded as significant in comparison with the control. The fact that no significant decrease in leaf size can be noted may be explained by the fact that treading produces consolidation in the first 2 or 3 cm. of soil only, below this level the density of the earth is comparable with that which is unconsolidated. The clover is able to force the strong tap root through this surface layer, and to spread its deep root system through the lower soil. It appears that the only effect of this surface consolidation is the restriction of the development of secondary roots in the region of this layer and the difficulty in establishing adventitious roots from runners, owing to the hardness of the soil surface. The root system as a whole was almost as well developed as in the control.

In the case of other species, such as grasses or other shallow rooting plants, this consolidation of the top layer of soil may restrict root range and leaf size. It has been shown (2) that where the soil has been consolidated to a depth of 40 cm. the whole plants of the several species grown were restricted in growth.

Strips 3 and 3 *a* showed the same result from treading the leaf as from cutting, though the reduction in size was not so great. The difference is probably explained by the fact that crushing by the foot does not effect so complete an obliteration of leaves as does the cutting, though this depends on the intensity of the treading.

In the case of strips 4 and 4 *a* the effect of cutting had a very rapid effect on leaf size. After the first cutting the second crop of leaves was smaller, and there was a steady but diminishing reduction after each subsequent cutting. Root range was restricted in development to a greater extent than in any other treatment.

The fact that in the case of strips 5 and 5 *a*, where the plants were root-pruned only, there was a great reduction in leaf size, comparable with that produced by cutting at weekly intervals, is of great significance. The result points to the fact that reduction in leaf size is not directly due to cutting or crushing of the leaf, but to the subsequent effect on root range and water supply, which in its turn automatically reduces leaf size.

In the case of the root-pruned strips the root is directly restricted without interference with foliage, but it is obviously impossible to reverse the process, i.e. to cut or crush the foliage without restricting root range, and it can therefore never be more than an assumption that cutting or crushing has no direct influence upon leaf size. But the effect of root pruning does definitely prove that root restriction can be fully responsible for diminution of leaf size, apart from any direct mechanical influence upon the leaf. As leaf size is reduced by root pruning to as great an extent as by cutting or crushing it does point to the fact that these latter processes do not reduce leaf size by any direct means.

It is worth noting that the different sizes of leaf on any clover plant, arbitrarily placed in two groups, large and small, exhibit a distinct stratification, i.e. an upper stratum of large leaves and a lower stratum of small leaves. It might be argued that the influence of cutting or treading in reducing leaf size simply depends upon the removal of the upper layer of large leaves; but this is disproved by the fact that root pruning also inhibits the formation of this upper stratum.

II. SOIL ACIDITY AND ITS INFLUENCE UPON ROOT STRUCTURE AND LEAF SIZE.

Influence of soil acidity on root structure.

It has been known for some time that *T. repens* tolerates a high degree of soil acidity (**3**). Observations upon very acid soils in the midlands and north of England showed that plants growing upon these soils possessed a comparatively smaller leaf than upon an alkaline soil, but there were a few puzzling exceptions.

On examining root structures it was noted that in some cases the whole root system was restricted in size, while in others it appeared to be better developed in some regions of the soil than in others—in other words to exhibit stratification.

In many soils there is a definite stratification of soil acidity due largely to biotic influences. Acidity may be more intense in the surface layers of the soil, owing to the formation of acids in the surface layer of dead root material or "mat," and the CO_2 from living roots. In industrial districts acid fumes may be the cause of this surface acidity, and may also assist indirectly in the formation of "mat."

Sometimes the acid surface layer is ploughed completely under, thus forming an acid stratum at some depth below the surface. Acid pans may also produce this effect.

Where liming has been carried out the surface layer of an acid soil may become alkaline or neutral in reaction in consequence of the liming.

A soil may also be acid throughout.

On examining root systems in the field, and at the same time making field tests of the intensity of acidity of the different layers of soil by means of soil indicator (approximate *p*H value determined by B.D.H. Universal Indicator); it was noted that the root system definitely reacted to the acidity of the soil at different depths. Root development was restricted in the most acid layers, and comparatively better developed in the alkaline, neutral, or less acid layers of the soil. There was also a definite inhibition of nodule formation in the most acid layers.

Experiments.

The stratification of soil acidity was never sharply defined in the field and no strict line of demarcation could be drawn. In many cases the *p*H value of one layer did not exhibit a wide range of difference from that in another. For this reason one could not take any measure (photographically or otherwise) of the corresponding stratification of the root system, but observation left no doubt as to its existence.

To confirm the above observations and produce definite evidence, experiments were set up as follows:

In the year 1928 plants of *T. repens* were grown in a garden soil of neutral reaction (*p*H 7 approx.) into which layers of very acid soil (*p*H 3 approx.) were introduced. The acid soil was, as nearly as possible, of the same physical texture as the alkaline. Both soils overlay Coal Measure shale, but the neutral soil owed its condition to frequent and heavy liming. The experiment was not carried out in pots, as this leads to a felt-like formation of root fibres against the surface of the pot. Garden borders were utilised.

When the plants had flowered and the seed formed, their root systems were examined by the following method: The plants were excavated, with the block of soil in which the roots were growing preserved intact. The block was wrapped with fine-mesh netting and pierced with wire skewers, to keep the roots in place. After the soil had dried it was shaken gently until all the particles fell away from the roots, any lumps adhering to the roots being crushed with the fingers. (The system of washing out the roots, adopted by some workers in the U.S.A. and U.S.S.R., was found impracticable, as it resulted in a felting together of the secondary roots.)

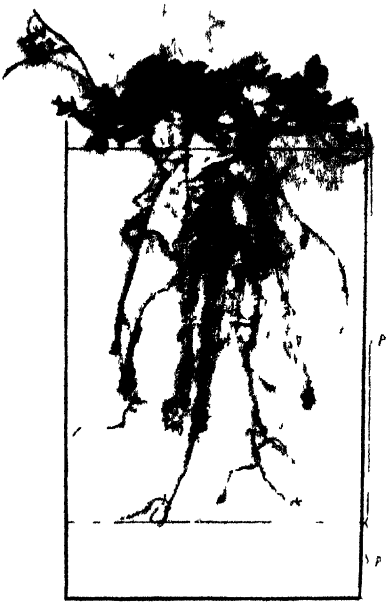
Phots. 1, 2 and 3 (Pl. XXIII) show clearly the reaction of the secondary roots to the stratification of acidity.

In the following year a similar experiment was carried out with the same results. The effect in the root systems of plants of *T. pratense* was also observed and the same reaction was noted.

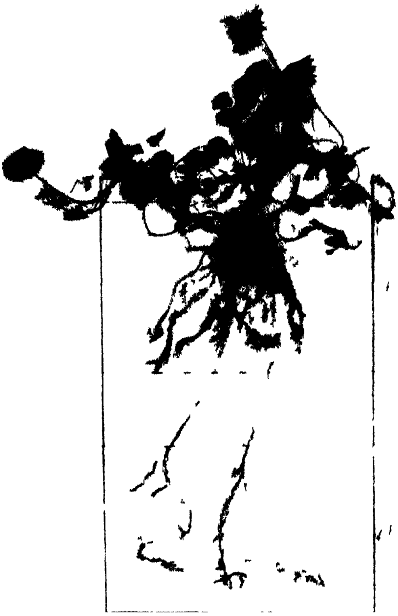
A further trial was carried out in 1931 on a sandy soil (approximately *p*H 6, with a lime content of 0·40 $CaCO_3$) into which layers of sandy acid soil (*p*H 3 approx., lime requirement 0·063 per cent. CaO) were introduced. In this trial dense patches of *T. repens* were grown by heavy seeding. Phots. 4, 5 and 6 (Pl. XXIV) show the same results as in the 1928 experiment (Phots. 1, 2 and 3).

Influence of soil acidity on leaf size.

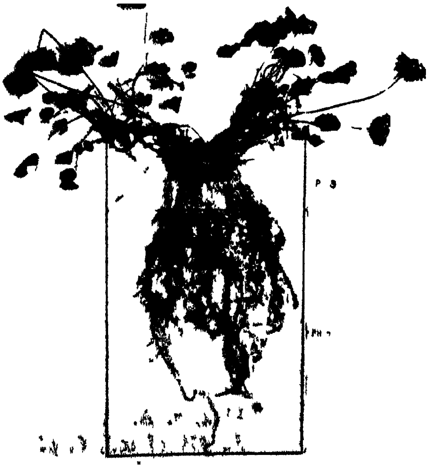
Observations in the field showed that where an alkaline surface layer overlay an acid soil the germination and establishment of *T. repens* and other cultivated plants was vigorous. It is now a generally accepted fact (4) that in the case of several grasses a thin layer of neutral or alkaline soil is sufficient to



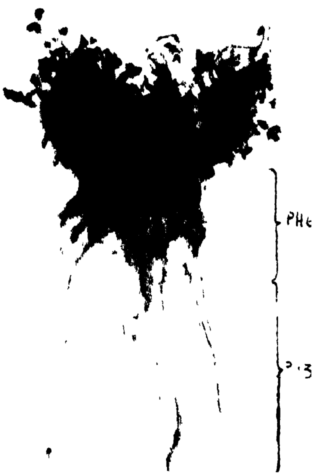
Phot. 1. Root structure in relation to soil acidity.



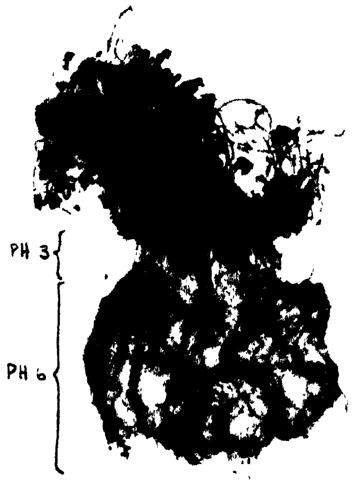
Phot. 2. Root structure in relation to soil acidity.



Phot. 3. Root structure in relation to soil acidity.



Phot 4. Root structure in relation to soil acidity.



Phot. 5. Root structure in relation to soil acidity.

Phot. 6. Root structure in relation to soil acidity

Phot. 7. A. *p*H of soil, 3, *p*H of surface layer, 6. B. *p*H of soil, 6, *p*H of surface layer, 3. C. All acid soil, *p*H 3.

BATES—*TRIFOLIUM REPENS*

stimulate germination and establishment on an acid soil. In the case of the establishment of *T. repens* under these conditions the plants in the early stages were vigorous as compared with those grown in an all-acid soil. This was demonstrated experimentally in pots, and is often observed in practice. It was noted, however, both in the field and in the pot experiments, that when a drought ensued, the plants withered, the larger leaves died off, and a smaller-leaved plant resulted, comparable with that grown in an all-acid soil. On examination it was found that the root system had largely developed in the alkaline surface soil, apparently at the expense of the root range.

When an acid layer occurred at a certain depth, the leaf size did not appear to be affected. The root range, as a whole, suffered no restriction, except in the acid layer itself, where there was little development of secondaries.

Experiments were set up in 1932 to confirm these observations, and to obtain definite data with regard to leaf size.

Plants were grown in (1) acid soil with a neutral surface layer, (2) neutral soil with an acid surface layer, (3) all acid soil, (4) all neutral soil: strips 1 and 1 *a* of the previous section of this work were taken as an example of an "all-neutral soil." This was the neutral soil used in (1) and (2) in this paragraph.

The figures set out in Table II show the differences in leaf size, the estimations being made in the manner previously described.

Table II.

Example	Soil	Average size of leaf sq. mm.	Range of leaf area sq. mm.	Average area expressed as %
1	Acid soil neutral surface	320	65– 763	51·0
2	Neutral soil acid surface	369	58– 983	58·8
3	All acid soil	280	61– 808	44·6
4	All neutral soil	627	75-1260	100·0

In example 1 leaf size was reduced in comparison with example 4. In example 2, which was checked in growth in the early stages owing to germination taking place in an acid medium, some relative reduction was noted, but in example 3 the leaf size was as much reduced as in example 1.

Phot. 7 A, B and C (Pl. XXIV) show the relative differences between 1, 2 and 3 of the above table.

SUMMARY.

It is shown that restriction of leaf size may be produced by the mechanical operation of cutting or crushing the leaf. These actions interfere with the nutrition of the root, thus affecting root range. A restricted root range results in a limited water supply, which automatically produces a smaller leaf, and consequently a smaller area of transpiration. Direct root pruning produces the same phenomenon.

Soil acidity may occur throughout the whole of the soil, or in strata. When acidity restricts root development, leaf size is also reduced, in proportion to the degree of root restriction.

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GRASSLAND RETROGRESSION IN DEVONSHIRE PERMANENT PASTURES

BY E. WYLLIE FENTON.

(*With two Diagrams in the Text.*)

CONTENTS.

	PAGE
Introduction	279
Method	280
Composition and classification of permanent pastures	280
Experimental	281
Field observations	283
Discussion	284
Summary	287
References	288

INTRODUCTION.

PERHAPS it is only right to state that the permanent pastures of Devonshire are not worse than those I have examined in most parts of Britain. In truth, the grasslands of Devonshire are among the best in Britain. The reason that the permanent pastures of Devon are selected is that I was resident in Devonshire for eight years and had therefore an unique opportunity of obtaining an intimate knowledge of its grasslands. Further, by confining the study to one county, climatic considerations are more nearly alike than they would be if examples were considered from scattered parts of Britain. The laying down of many experimental (manured) plots of the long narrow shape (**6**), in permanent pastures in almost every part of Devon, provided ample opportunities to watch the process of improvement which occurred, and to record the changes in vegetation. Examples of retrogression[1] were also under observation during the same period. The present paper is a rather condensed account of the information obtained from this source as far as it concerns ecology.

The first point which had to be decided before the investigation had gone far was to define what should be considered a permanent pasture, and what a permanent grassland. A permanent pasture may be defined as any area of grassland which has been under continuous pasturage for many years and is not more than 15–20 acres in extent. Only a few of those I examined were over 15 acres. The reason for this decision is that greater areas cannot or will not be controlled by the farmer. Hence beyond this limit it seems impossible adequately to control the grazing and any other factors which enter into the problem. Beyond this limit grassland is considered as permanent grassland so as to differentiate it from permanent pasture. Many examples of the former have been dealt with by Stapledon (**17**).

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[1] The term "retrogression" is used in this paper in the agricultural sense. Ecologically, of course, the succession to scrub and woodland is *progression*.

METHOD.

It was obvious that a method of botanical investigation and analysis must be selected which would avoid laborious and tedious work in a laboratory, since the time spent in the open must be long and continuous. Such consideration left no choice but to adopt the grid method (**1**), which I applied in similar manner to that adopted in investigating grasslands in Scotland (**7**).

The grid method has many advantages, since it records the percentage of ground covered by each species present in the area examined. It is in fact, an aerial survey of a Lilliputian forest—a grassland area. In a well-grazed field it is a race of recovery among the "topped" plants in which the more nutritious plants keep the lead, but in badly grazed fields the grazed plants suffer while the ungrazed do not lose their top canopy. When grazing is very light or nil, top canopy plays practically as important a part in determining the vegetation as it does in a forest.

COMPOSITION AND CLASSIFICATION OF PERMANENT PASTURES.

It was evident, even in the early stages of the investigation, that when the composition of permanent pastures was analysed the pastures could be readily grouped according to the species which were dominant and sub-dominant. These determining species normally gave the pastures a distinctive appearance. An early preliminary survey of this problem was dealt with from the agricultural side some years ago (**11**).

The best permanent pastures were those in which the vegetation consisted chiefly of *Lolium perenne* plus *Trifolium repens* as Armstrong (**1**) showed some years ago, as Fream (**12, 13**), Carruthers (**3, 4, 5**) and McAlpine (**15**) had noted in earlier times and as was recently again verified by myself (**7**). This type was considered as group I, the ideal—from the farmer's point of view—and all others were derived from this ideal by retrogression. Any permanent pasture in which *Lolium perenne* plus *Trifolium repens* were dominant or in higher proportion than any of the other species was placed in this group. Occasionally other valuable grass may replace *Lolium*, such as *Poa* spp. and in the early stages *Dactylis glomerata*, *Phleum pratense* and *Alopecurus pratensis*, etc. Group I is ecologically a deflected succession (**14**) derived from arable land.

Group II pastures were those where *Trifolium repens* was still dominant but where *Agrostis* spp. were sub-dominant. On the border line between this and group III were pastures where *Agrostis* spp. were dominant and *Trifolium repens* sub-dominant. In both cases *Lolium perenne* was present, often ranging from 10 to 15 per cent. of the ground covered.

Group III was a large one necessitating the division of the group into four classes A, B, C and D. In all classes *Agrostis* spp. were dominant; but in class A *Holcus lanatus* was sub-dominant; in class B *Cynosurus cristatus* was sub-dominant; in class C *Anthoxanthum odoratum* was sub-dominant; and class D was distinguished by the presence of many heath plants. Class D was derived from any of the classes A, B or C. Class A also included a few examples where *Holcus lanatus* became dominant and *Agrostis* sub-dominant. For the most part class A occurred where moisture was plentiful, the soil acid, and there was selective grazing. Class B was found to consist of areas in which the soil was generally heavy and moist, or where there was a copious rainfall, or *Cynosurus* was not cut down before seeding. Generally, grazing was selective and too light. Class C contains those pastures where the soil was light or where drought was of frequent occurrence. The presence of such plants as *Luzula campestris*, often in appreciable quantity, further emphasised the dry nature of the pasture. These classes may occasionally interchange with different treatment and altered methods of stocking, but this is not of frequent occurrence.

Group IV is distinguished by the varied, weedy, poor and often starved vegetation, with much ground which is bare. It is usually the high proportion of bare space which is its chief characteristic. *Agrostis* spp. are often prominent.

Group V is distinguished by the presence in quantity of *Agrostis* spp. and *Festuca ovina* (agg.). In class A *Agrostis* spp. are dominant and in class B *Festuca ovina* (agg.) is dominant.

Group VI is what is often described as heathy grasslands where *Agrostis* may be present in quantity, but the total amount of heath plants is generally greater than that of the more useful grasses.

Group VII is scrub grassland. The permanent pastures of this group are easily identified by the masses of shrubby plants and sometimes trees which may occupy at times more than half the total area.

There is finally the climax of either heath or scrub-woodland leading to woodland.

EXPERIMENTAL.

(Diagram I.)

The County Organiser (Mr C. D. Ross) and his staff laid down a series of long narrow plots in permanent pastures selected for investigation, and treated these with different phosphates (yielding equivalent quantities of phosphorus), some with a cross dressing of lime and occasionally potash. The vegetation after this treatment was compared with control plots. In the favourable Devonshire climate results were obtained very quickly, and it became possible to trace the changes and thus to piece together (in the reverse direction) how retrogression had occurred. The manured plots were open to grazing animals, and the best plots were those most heavily grazed—a rather important point since it indicates the value of the method of botanical analysis adopted. Our estimations of the plots botanically were in agreement with the farmer's based on the grazing of the stock.

Where grazing was withheld, the vegetation retrogressed, and even the application of manures failed to arrest retrogression till long after grazing was again commenced. This showed very clearly the important rôle of the grazing animal (**9**, **10**). When grazing was too light, manures had no appreciable effect. The general result, as Diagram I shows, is that the chief deficiency of most permanent pastures is phosphates and lime. The best permanent pastures, showing practically no variation from year to year, were those which received the best treatment and the most skilful grazing. In fact they were treated as all "sectional" grazed and manured plots should be treated if they are to be successful (**8**). The extraordinarily rapid improvement of, and the high quality of vegetation attained by, many of these exceedingly poor permanent pastures within the short period of three years came as a distinct surprise. It stresses once more the importance of the maintenance of fertility and of the skilled handling of grazing animals.

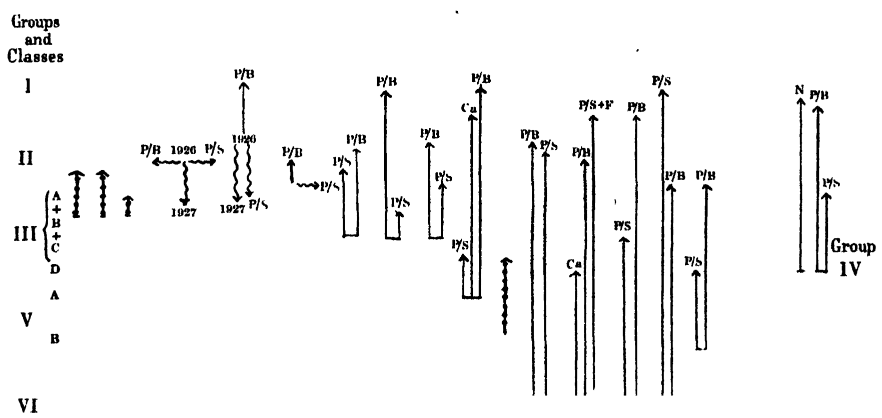

Diagram I. Diagram showing changes in vegetation of pastures induced by grazing and manuring. Vegetation indicated by groups and classes. ↑ Grazing and manure; ⇡ Grazing alone; ⇣ Inadequate or no grazing; P/B Basic slag; P/S Superphosphate; P/S + F Superphosphate + Steam bone flour; Ca Lime; N Nitrogen (farmyard manure).

Another very important fact was revealed in these improvements. Naturally all plots did not show the same degree of improvement: some plots developed a fine vegetation totally different from the original, while others showed little improvement and others ranged between the two extremes. It was noted that all the plots in any permanent pasture tended to pass through the same phases during improvement. They all passed to a better vegetation *via* group III *a*, III *b* or III *c*. It was a comparatively rare occurrence for improvement to follow two different paths, although examples did occur where it was difficult to place the progress in any of these three classes. These borderline cases will be found among permanent pastures which in the process of their change have temporarily settled down.

Examples occurred where improvement was delayed and also where the results were not in accordance either with expectations or the general average of the county. That, however, raises questions (chiefly of a chemical nature) which cannot be discussed here. As has been found elsewhere, liming in some cases made matters worse for a time owing to the violent changes caused in the soil and the vegetation. After this initial fluctuation, however, most of the limed areas showed a steady improvement. In many cases lime produced a very marked change, as Diagram I shows. There were a few instances of potash improvement; and although only shown in the diagram in one example of group IV, nitrogen in some cases made almost as much and as rapid an improvement as liming.

FIELD OBSERVATIONS.

(Diagram II.)

It became quite obvious that the changes in the vegetation of the plots showed a distinct movement and a passage through certain phases in the process. In other words the experimental evidence verified the field observations by reversing the process. As grassland retrogressed from group I to group II it meant a slow loss of fertility. Group III was derived from group II by a slightly more rapid loss of fertility due primarily to neglect. In group III grazing is generally inadequate and often too selective.

From class D of group III is derived group V. Permanent pastures of this group are found chiefly at higher elevations or on dry heathy lands. This is by no means universal, for we have found pastures of this group quite near good pastures, but neglect was the chief cause and not soil conditions or exposure. Occasionally the *Agrostis-Festuca* combination becomes so dominant as almost to exclude all other species. This group may retrogress to group VI if there is not adequate grazing.

Group VI consists of those permanent pastures which are virtually heaths. Only the light and inadequate grazing prevents the vegetation reverting to a typical heath or perhaps wood. There are usually appreciable quantities of *Calluna vulgaris*, *Erica*, *Triodia*, *Nardus*, etc. Permanent pastures in group VI may possibly be derived from group III, class D, but so far we have not sufficient evidence beyond one or two examples, which are not without doubt.

Group IV contains permanent pastures which retrogress by what may almost be considered a short circuit. This is due to a rapid exhaustion of the soil by cutting a succession of hay crops for several years. The result is that finally almost 50 per cent.—and often more—of the surface of the permanent pasture may be bare soil. This group may arise either from group I or group II. In the old times it arose from derelict arable land. Permanent pastures of this group may also arise from the failure of the seeds mixture. This, of course, means a "thin plant" with much bare space. It is not of frequent occurrence now, as a renovation seeding, or ploughing up and re-seeding, is the general custom. If the grazing of such permanent pastures is light retrogression proceeds to group V. If on the other hand—as does happen—there is no grazing, then retrogression leads to group VII.

Group VII consists of permanent pastures which have retrogressed from group IV and may also be derived from class C, group III, where there is either no grazing or the grazing is inadequate to cause the suppression of shrub or tree growth.

With the cessation of grazing groups VI and VII slowly pass to the climax of either heath or a scrub-wood, which may end in a wood, as illustrated in Diagram II.

The correct identification of *Agrostis* species in the field and in the vegetative stage is virtually impossible and for this reason the species are not distinguished, but grouped. There is extraordinary variation, which suggests crossing, and much modification according to environment. I have adopted the classification of Bentham and Hooker, grouping the various forms under *Agrostis palustris* Huds. This is equivalent to *A. alba* L., which is frequent and widespread, as well as *A. stolonifera*, very common in permanent pasture when moisture is plentiful. *A. tenuis* Sibth. (= *A. vulgaris* With.) tends to occur in dry situations, while as heathy conditions develop *A. canina* L. begins and becomes more frequent as heath approaches and also as the elevation increases. *A. setacea* Curt. was found occasionally in Cornwall.

DISCUSSION.

Besides the changes due to grazing and manuring, i.e. the inversion of the retrogression due to improvement, many cases where the retrogression could be traced were found. Some examples were verified where an open scrub-woodland with grass was about eighty years ago under wheat, others occurred where the changes had not gone so far, and many where the movement was actually traced though only to a limited extent. In one case on Sellick Moor the change from group VI to an *Erica* heath took place in three years.

As Diagram II shows, the types of permanent pasture are very well marked, but the actual flora shows the presence of the same plants in practically all examples from group I till group III *c* is reached, to which must often be added group IV and perhaps group VII. Groups III *d*, V and VI lie outside this similarity, for the better grasses and clovers are usually absent. Hence it is that groups I–III must be considered neutral grassland association (Graminetum neutrale) (**18**) and can be definitely placed in its position in British vegetation as belonging to a definite association. Group V is well known on chalk and in other xerophytic conditions (**18**). Group VII, excluding the scrub, may belong to Graminetum neutrale, as does group IV, but group VI is more nearly allied to group V and is really the borderline between it and the typical heath. A recent example of a group V pasture which had been neglected showed both some shrubby growth (*Rubus fruticosus*) and *Calluna vulgaris* gaining an entrance and indicating the beginning of the group VI phase (**10**).

As Diagram II shows, retrogression is accompanied by increasing deficiency of lime (calcium), phosphates and available nitrogen. Simultaneously yield

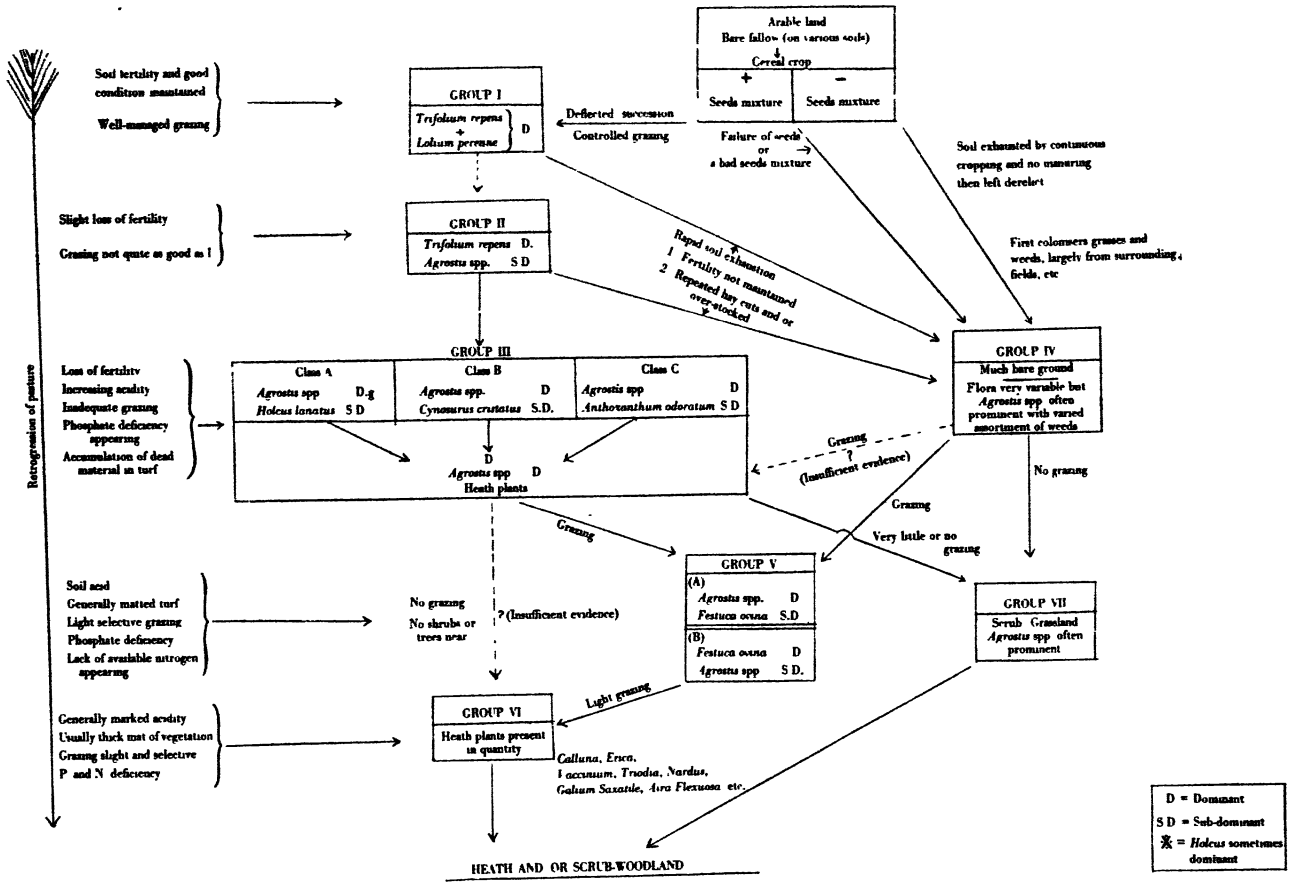
Retrogression of pasture
Soil fertility and good condition maintained
Well-managed grazing
Slight loss of fertility
Grazing not quite as good as I
Loss of fertility
Increasing acidity
Inadequate grazing
Phosphate deficiency appearing
Accumulation of dead material in turf
Soil acid
Generally matted turf
Light selective grazing
Phosphate deficiency
Lack of available nitrogen appearing
Generally marked acidity
Usually thick mat of vegetation
Grazing slight and selective
P and N deficiency
GROUP I
Trifolium repens + Lolium perenne D
GROUP II
Trifolium repens D.
Agrostis spp. S D
GROUP III
Class A
Agrostis spp D.※
Holcus lanatus S D
Class B
Agrostis spp. D
Cynosurus cristatus S.D.
Class C
Agrostis spp D
Anthoxanthum odoratum S D
D
Agrostis spp D
Heath plants
Arable land
Bare fallow (on various soils)
Cereal crop
+
Seeds mixture
−
Seeds mixture
Deflected succession
Controlled grazing
Failure of seeds or a bad seeds mixture
Soil exhausted by continuous cropping and no manuring then left derelict
First colonisers grasses and weeds, largely from surrounding fields, etc
Rapid soil exhaustion
1 Fertility not maintained
2 Repeated hay cuts and or over-stocked
GROUP IV
Much bare ground
Flora very variable but Agrostis spp often prominent with varied assortment of weeds
Grazing ? (Insufficient evidence)
No grazing
Grazing
Very little or no grazing
Grazing
GROUP V
(A)
Agrostis spp. D
Festuca ovina S.D
(B)
Festuca ovina D
Agrostis spp S D.
GROUP VII
Scrub Grassland
Agrostis spp often prominent
No grazing
No shrubs or trees near
? (Insufficient evidence)
Light grazing
GROUP VI
Heath plants present in quantity
Calluna, Erica, Vaccinium, Triodia, Nardus, Galium Saxatile, Aira Flexuosa etc.
HEATH AND OR SCRUB-WOODLAND
D = Dominant
S D = Sub-dominant
※ = Holcus sometimes dominant

DIAGRAM II. Illustrating retrogression of pasture to heath and/or scrub-woodland as the result of inadequate grazing.

and palatability are lowered, making adequate grazing more difficult. The whole problem, therefore, tends to get progressively worse till a stage of mineral deficiency is almost reached (**16**).

Lack of proper drainage is a serious problem and a frequent cause of retrogression. In a few pastures we found that a flora suggesting a serious lime deficiency was caused by faulty drainage. The soil on test showed no lime requirement, but as soon as drainage was begun the flora completely changed and in place of a group III *d* flora with marshy patches, a group II flora rapidly developed and was moving towards the lower reaches of group I.

"Laying" does occur in grassland, but only becomes serious when the growth becomes too long. In good permanent pastures the best grasses and clovers recover too quickly after grazing to permit any inferior plants from offering serious competition. As the soil becomes less fertile the inferior grasses and other plants are better able to compete; selective grazing unduly punishes the more valuable grasses and clovers, so that they are gradually overwhelmed by the other species present. Under these conditions stunted specimens of the better grasses and wild white clover may be found struggling towards the light, while *Agrostis* spp. and other inferior grasses and plants shade these out and retard their early spring growth with the covering of leaves and stems encumbering the surface vegetation. In time this forms a mat of undecayed vegetation on ungrazed pasture till it is difficult for water to penetrate to the soil and finally an almost peat-like formation may begin to develop. This becomes increasingly evident as one passes from group III to group VI.

It must not be forgotten that all permanent pasture cannot be "improved" to group I or even group II. Altitude, exposure, soil, and climate all play a part and may act as limiting factors, particularly from an economic aspect. Conversely, all permanent pastures may not retrogress to the final climax, since biotic and/or edaphic conditions may prevent this occurrence. As grassland retrogresses, the soil plays an increasing rôle in determining the nature of the vegetation. This becomes evident as soon as retrogression reaches group III. Another interesting point is that groups I, II and much of III correspond respectively very closely to the agricultural classification of first, second and third class permanent pasture (**17**).

This retrogression of permanent pastures and permanent grasslands is a constant menace to both good grasslands and arable land, for poor areas harbour obnoxious pests, both plant and animal. There is a constant invasion of the seeds of inferior plants (including shrubs and trees) into the better grasslands. There is little doubt that the marked decrease of store cattle has much to do with this problem and the spread of bracken. This is not entirely due to grazing but also to the trampling action of the cattle. About twenty years ago I saw considerable areas of scrub grassland in Scotland most successfully broken in to good pasture chiefly by the judicious use of store cattle followed by manurial and other treatment. This is still being accomplished in Wales (**2**), but seldom occurs now in most parts of Britain. Until such areas are brought under control there is little hope of great improvement. The chief problem is the grazing animal. To exercise control means greatly increased stocking or virtually the running wild of sufficient stock to keep the vegetation under control, while draining, manuring, and mechanical treatment must not be overlooked. There seem to be two choices: either the nature and kind of the stocking must be in keeping with the vegetation and what it will support, or fertility must be improved and maintained to support the stock required and to keep the vegetation in good order.

The small proportion of British to the total meat and meat products consumed in this country is tragic when our grasslands could carry many more grazing animals. It is surely a matter demanding investigation including the problem of "winter keep." If stock increase the grasslands improve, and if stock decreases grasslands retrogress. It shows how worldwide influences of an economic nature influence the grassland vegetation of this country. Until it is realised that the problem is ecological, there is practically no hope of any real or fundamental progress.

SUMMARY.

Permanent pastures are defined and limited to an area of 15–20 acres.

Permanent grasslands can readily be placed in the following groups:

Group I. *Lolium perenne* and *Trifolium repens* dominant.
Group II. *Trifolium repens* dominant and *Agrostis* spp. sub-dominant.
Group III. Class A. *Agrostis* spp. dominant. *Holcus lanatus* sub-dominant.
Class B. *Agrostis* spp. dominant. *Cynosurus cristatus* sub-dominant.
Class C. *Agrostis* spp. dominant. *Anthoxanthum odoratum* sub-dominant.
Class D. *Agrostis* spp. dominant, plus many heath plants.
Group IV. High proportion of bare ground.
Group V. Class A. *Agrostis* spp. dominant. *Festuca ovina* (agg.) sub-dominant.
Class B. *Festuca ovina* (agg.) dominant. *Agrostis* spp. sub-dominant.
Group VI. High proportion of *Erica*, *Calluna*, *Nardus*, etc.
Group VII. Trees and/or shrubs and grassland.
Groups I–IV plus VII rank as neutral grassland association.

Grasslands retrogress in sequence through these groups and classes and improve in the reverse direction.

Economic conditions influence the vegetation of permanent pastures by increasing or decreasing the number and kind of the grazing animals. The problem can only be solved by a careful ecological study.

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THE RATE OF DECAY IN RELATION TO SOIL TYPES AND VEGETATIVE COVERING IN GLAMORGAN

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THE investigation of the rate of decay in Glamorganshire soils was undertaken with a view to ascertaining the extent to which the decomposing power of soils within a climatic region is affected by the geological character of the rocks from which the soils are derived, and also by the character of the vegetative covering.

The climate of the county as a whole is moist and equable, but due to the fact that the county has a varied topography (having three natural regions) the climatic conditions show a fair range of variation. The average rainfall varies from 40 in. in the southern plain to over 80 in. per annum on the plateau of north Glamorgan. The southern plain and the northern plateau also present a contrast geologically, for Pennant Grits are the predominating surface formation in the highland country, while the dominant surface formation of the comparatively low-lying plain to the south is Lower Lias. Most of the work was carried out on soils from the southern part of the county. There are not many data available concerning the climatic status of Glamorganshire soils, but the little evidence which the writer was able to collect indicates the soils of south Glamorgan to be Brown Earth types (Ramann's classification[1]).

The rate of decay was measured in terms of carbon dioxide evolution, which has proved to be one of the best and most convenient indices of the rate of decay in soils. Linseed meal was added to the soil to the extent of 1·5 per cent. of the dry weight, and the water content was made up to 50 per cent. of the maximum water capacity of the soil. Linseed meal was chosen, since a rapid decay can be predicted from the easy accessibility of mucilage and aleuron grains due to its crushed condition, and from the satisfactory ratio of available carbohydrates (energy factor) to lignin (resistant factor). We may also note that the nitrogen content of linseed meal is well above the limit where nitrogen content acts as a limiting factor in soil biochemical processes.

The most outstanding result that has emerged from the present work is that the rate of decay in a soil shows a well-marked seasonal periodicity, with maxima occurring in spring and autumn, and depressions in winter and summer, the winter depression being very marked—a result which was obtained in spite of the fact that the soils during the experimental period were kept under standard conditions of temperature and humidity. This result—which was worked out most fully in the case of Lower Lias soil—accords with other seasonal periodicities that have been worked out for the soil, such as the seasonal rhythm in bacterial and protozoan numbers and the seasonal variation in the carbon dioxide content of the soil atmosphere. In fact the seasonal variation in decay which is shown by a single soil exceeds the differences in power of decomposition of different soils within the county to a marked degree. It would thus seem of importance to take season into account in interpreting and comparing the rate of decay in soils.

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[1] **Ramann, E.**, *Bodenbildung und Bodeneinteilung*, Eng. trans. by C. L. Whittles, 1928 (*The Evolution and Classification of Soils*).

The differences in decomposing power of the various soils studied were not great but quite definite in character. The soils investigated can be arranged in the following order of increasing power of decomposition:

Devonian heath and Pennant Grit;
Carboniferous Limestone;
Triassic Breccia B, Devonian woodland, and Lower Lias woodland;
Lower Lias semi-scrubland;
Marine alluvium;
Triassic Limestone Breccia A.

An examination of the above series shows that most of the soils examined have a lower decomposing power than Lower Lias semi-scrubland soil, but Triassic Breccia B, Devonian woodland and Lower Lias woodland soils have a decomposing power not much inferior to it.

It may surprise some readers to find soil over Carboniferous Limestone so low in the list of decomposing powers, as investigations have shown that lime has a stimulating effect on decay, and indeed this is recognised in agricultural practice. The Carboniferous Limestone soils of south Wales that were studied gave blank results when tested for carbonates, and the pH was on the acid side of neutrality. These properties of the soil were reflected in the vegetation, the most prominent plants being *Pteris aquilina*, *Ulex*, *Erica* and *Calluna vulgaris*. These soils, however, although lacking calcium carbonate are not entirely devoid of calcium in other forms, for they do not develop any colour in contact with an alcoholic solution of potassium thiocyanate (Comber's test), and for the most part they give little or no colour with ammonia solution. This view is confirmed by the authors of the soil survey of Wales who, dealing with the soils from an agricultural point of view, pointed out that although calcium carbonate may be absent from the soils of south Glamorgan, the lime status of these soils appears to be generally satisfactory[1].

Different types of vegetative covering on soils derived from the same parent rock may exercise a slight (Lower Lias) or considerable (Devonian Red Marl) modifying effect on the power of decomposition.

The course of decay is usually marked by a rise to a maximum within the first few days of incubation, after which there is a gradual drop. The time and intensity of the maximum varied with the season (as well as to some extent with the soil). The greater the intensity of carbon dioxide evolution the more marked in general was the maximum. With a lower carbon dioxide output there was a tendency for the maximum to be delayed and blunted. In a few cases where the soil was in a dry condition at the time of collection, the maximum carbon dioxide evolution occurred on the first day of incubation, which may be accounted for by the fact that the addition of water to air-dry soil brings about a rapid increase in carbon dioxide evolution followed by a gradual drop[1]. These instances would indicate that weather conditions may not be without effect on the course of decay in soil. In some experiments a second and lesser maximum of decomposition was indicated. Linseed meal contains many organic complexes and this second maximum may represent a real maximum intensity of decomposition of one or more organic constituents.

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[1] Robinson, G. W., Jones, J. O. and Hughes, D. O., "Soil survey of Wales," Progress Report, 1925–7, *Welsh Journ. Agric.* 4, 3–21, 1928.

Most of the work done on decay in soils has been carried out in relation to the study of soil fertility, and thus it is of interest to enquire to what extent the fertility of the soils investigated runs parallel to the intensity of carbon dioxide evolution during the decomposition of linseed meal. A difficulty presents itself immediately, for throughout this investigation "agricultural land" was avoided and in no case was cultivated land dealt with, although it was recognised that land which is now covered by natural vegetation may a few generations ago have been under cultivation. The authors of the "Soil survey of Wales" have characterised the soils of south Glamorgan in terms of agricultural fertility, and upon this basis it may be said that, in general, increasing fertility runs parallel with increasing power of decomposition of linseed meal. This view is, however, based on slender evidence, and experiments with cultivated soils of known fertility are necessary before any definite statement can be made.

The course of carbon dioxide evolution from a soil can be studied with or without the addition of organic matter, in the latter case the rate of carbon dioxide evolution being frequently known as the respiration rate of the soil. The present investigation has borne out the results of previous investigators that the differences in respiration rates of different soils are much more marked than the differences in power of decomposition. Also there is frequently a very marked difference between the respiratory and decomposing power of a single soil, a difference which is of a higher order than the differences between the decomposing power of different soils. The most extreme case encountered was that of a *Terra Rossa*[2] over Carboniferous Limestone in the Gower peninsula, the ratio of respiratory power to decomposing power being 1:21.

The form of the respiration curve was found to be constant, the maximum occurring on the first day of incubation and being followed by a very marked fall to a more or less constant level[3].

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[1] **Klein, M. A.**, "Studies in the drying of soils," *Journ. Amer. Soc. Agron.* **7**, 49–77.

[2] *Terra Rossa* is a soil type which is characteristic of warmer regions such as over limestone in the eastern Mediterranean. In the northern hemisphere, however, more southern soil types penetrate furthest north on limestone.

[3] For more detailed information, see *Journ. Agric. Sci.*, **23**, 31–72.

A NOTE ON THE FORESHORE VEGETATION IN THE NEIGHBOURHOOD OF GEORGETOWN, BRITISH GUIANA, WITH ESPECIAL REFERENCE TO *SPARTINA BRASILIENSIS*

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(*With Plates XXV and XXVI and one Diagram in the Text.*)

CONTENTS.

	PAGE
Introduction	292
The coast	292
The foreshore	293
The formation of the foreshore	293
The area under observation	294
The vegetation of the foreshore	294
The mud banks	294
The sandy "beaches"	295
The "lagoons"	296
The *Spartina* society	296
Comparison with *S. Townsendii*	296
History of the development of the society	297
Experiments with *S. Townsendii*	298
Summary	298
Acknowledgments	298

Introduction.

Rapid silting and the consequent recent formation of a foreshore, which has quickly become covered with vegetation, has been the object of some observations made by the writer in the neighbourhood of Georgetown, British Guiana. Before describing the vegetation in any detail, however, it may be as well to give a short account of the coast as a whole and of the factors concerned in the recent making up of the foreshore on parts of it.

The coast. The coast of British Guiana consists of a flat alluvial plain, laid down through the course of ages by the deposition of sea-borne clays, the greater part of which are considered to have originated in the effluent of the River Amazon, and to have been carried to their present site by the prevailing currents of the Atlantic. This plain extends inland for a distance varying from 10 to 40 miles before rising to any extent above sea-level, and is traversed by several rivers. Large areas near to the sea are below spring tide high-water level and are therefore liable to constant flooding. Narrow sand reefs here and there mark the sites of earlier shore-lines.

Before the advent of the early settlers, the whole coast was fringed by a belt of mangrove[1] swamp, behind which lay swamp savannahs, usually flooded, and occupied by sedges and numerous aquatic plants, *Mauritia flexuosa*, the "Aete Palm," being scattered throughout. As the level became slightly raised, a low type of swampy forest occurred. All these types of vegetation may be found to-day over large areas of the coastal plain, but since the advent of European settlers in the early part of the seventeenth century, this coastal belt has become the principal seat of agriculture, proving eminently suited to the cultivation of sugar, cocoa and other crops, including, more recently, rice. As a consequence, its vegetational aspect has been largely altered by the hand of man.

The early colonists were chiefly the Dutch, who, finding themselves in a country the physical features of which closely resembled their own home, adopted similar methods for the reclamation of land to those in vogue with their kinsmen in Holland. These methods are maintained in principle to the present day. The area of land to be "taken in" is "empoldered," i.e. surrounded by a dam to keep out water from the landward side, and a sea wall is built to protect it from the ocean (or river). The area so cut off is intersected by irrigation and drainage trenches, and drained by means of a "koker" or sluice in the sea wall, which is opened as the tide falls. Behind the sea wall conditions are therefore artificial: outside it, a natural foreshore may be formed.

The foreshore. Owing to frequent changes in the currents, the actual shoreline of the coast is constantly varying from point to point. In one section high tides may be menacing the sea defences, whereas a few miles farther along silting is taking place, resulting in the deposition of a new area of foreshore. As the currents change again, the newly formed land in turn becomes subject to erosion, and so the fluctuation continues. On such muddy areas, outside the sea wall, a "mangrove" association soon becomes established, in which *Avicennia nitida* (known locally as "Courida") usually predominates, intermixed with *Laguncularia racemosa*. *Rhizophora* spp., though dominant on the lower reaches of the rivers, are not so plentiful on these quickly formed areas of foreshore. Where mud is being rapidly deposited, however, it is to be observed that on parts of the coast *Spartina brasiliensis* Raddi plays a very considerable part in the primary colonisation of the rising mud banks. Owing to its similarity to *S. Townsendii*, which has of recent years attracted so much attention as a coloniser of muddy foreshores in European waters, a description of the succession that occurs in the building up of the foreshore association on parts of this coast may be of interest.

The formation of the foreshore. The manner in which the foreshore is laid down outside the sea wall is worthy of note, because not only does it decide the distribution of the societies within the association, but it also repeats, on a small scale, the process by which the whole coastal plain must have originally been formed.

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[1] The term "mangrove" as used throughout covers the several constituents of this association, including *Rhizophora* spp., *Avicennia nitida* and *Laguncularia racemosa*.

Where rapid silting is taking place, the greater part of the foreshore laid down consists of soft mud, which is deposited to form a bank stretching out from the sea wall. With the receding ebb tides, however, a certain amount of "washing" occurs in places at the foot of the wall, resulting in the formation of a shallow channel between the wall and the mud bank. This channel may in time be obliterated by mud being pushed over it, or may eventually form a sort of miniature "lagoon" behind the broadening mud bank. In addition to the mud, however, sand constitutes an important factor in these areas. Sand and broken shell from banks a short way out to sea are brought in by spring tides and wave action, carried over the mud bank and deposited inshore. The ultimate result is the formation of small sandy beaches at intervals along the sea wall, and the admixture of a quantity of sand and shell with the mud in the "lagoons" behind the mud bank, giving the mud there a much firmer consistency.

The area under observation. The portion of the coast on which these observations were made is a stretch some 10 miles in length, immediately to the east of Georgetown and the mouth of the Demerara River. In 1915 the sea defences on this frontage were seriously threatened, as a result of which the sea dam was strengthened by a concrete wall, and groins constructed to encourage silting. Subsequently, considerable silting has taken place, increasing in amount during recent years, and resulting in the deposition of a muddy foreshore, with a covering of vegetation, that stretches out from the sea wall for a distance varying from 100 to 300 yards.

THE VEGETATION OF THE FORESHORE.

(Pl. XXV, Phot. 1.)

The "foreshore association" consists of three societies, dependent upon three different types of habitat, which may be dealt with separately. These, as explained above, are

(*a*) The *mud banks* to seaward;
(*b*) The *sandy "beach"* at the foot of the sea wall;
(*c*) The intermediate *"lagoons."*

The mud banks (Pl. XXVI, phot. 3). These consist of soft mud, and their level gradually rises with continued deposition of silt. At first only exposed at low tide, as the level rises the highest contour is covered by spring tides alone. If the bank continues to the foot of the sea wall, the highest level is found here. If, however, a "lagoon" intervenes, the mud bank forms a ridge a little way out from the wall.

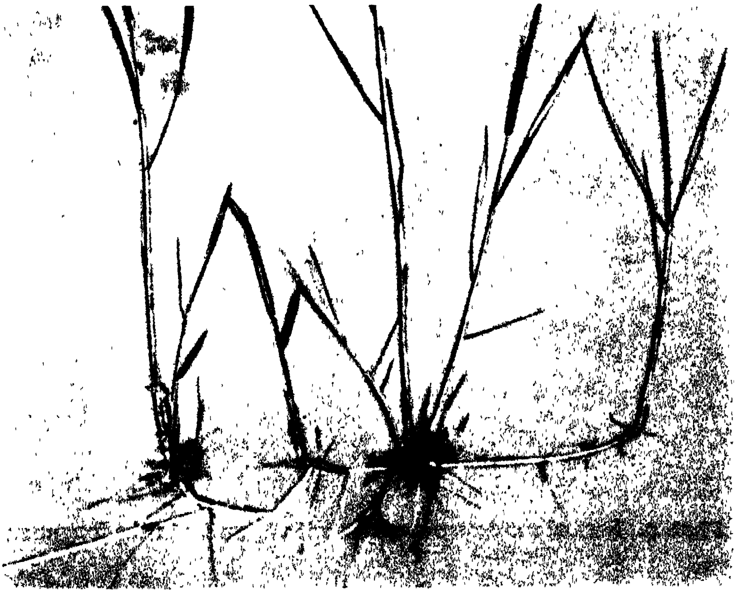
The mud is deposited more or less evenly, but as the level rises the retreating waters of the ebb tide carve out a network of small channels, leaving

Phot. 1. A general view of the foreshore from the sea wall. Sandy beach with *Ipomoea biloba* in foreground. "Lagoon" and grazed mangrove bushes behind the groyne in the middle distance; mud bank and belt of young mangrove in the background

Phot. 2. Part of the mangrove belt, with *Spartina* in the foreground.

MARTYN—*Spartina brasiliensis*

Phot. 3. The seaward edge of the mud bank. Primary clumps of *Spartina* in the background.



Phot. 4. Plants of *Spartina brasiliensis*, showing stolons, surface roots and anchoring roots.

MARTYN—*SPARTINA BRASILIENSIS*

islands of mud between. On these islets, *Spartina brasiliensis* gains a footing, either becoming established by portions of the plant, capable of vegetative reproduction, which are washed up from elsewhere, or by seedlings. Once established, with their system of surface feeding roots, deeper anchoring roots, and prolific production of stolons (Pl. XXVI, phot. 4), large clumps are soon developed. These raise the level of the mud and gradually unite, so that a little farther inland the separate islets give way to an almost pure stand of *Spartina*, intersected here and there by channels, in which are scattered seedlings of *Avicennia nitida* and *Laguncularia racemosa*. By the time this stage is reached, the level of the mud has been raised so that the highest portion is not covered by normal tides, and a tide mark, indicated by a line of drift débris, becomes definable. At this high-water mark, seeds of *Avicennia* and *Laguncularia* are deposited in the greatest profusion, resulting in an increase in the number of these "mangrove" plants, either at the foot of the sea wall, or as a very distinct belt of bushes along the top of the mud bank ridge, on the seaward side of a "lagoon" (Pl. XXV, phot. 1, 2). Once established, these plants of the mangrove association climax grow very quickly[1], becoming dominant to the *Spartina*, which finally almost entirely disappears beneath them. Two biotic factors however may hinder the "mangrove" from attaining its maximum development. The first is the grazing of cattle and goats, etc., on the foreshore. Where the mud bank is backed by a lagoon, the admixture of sand is such that the mud will support the animals' weight, and "mangrove" trees on the inland edge of the bank are kept closely grazed back, remaining as small squat bushes. In addition to this, as the trees on the mud bank itself reach a moderate size, they are cut back, both to supply firewood, and to control the breeding of mosquitoes.

The sandy "beaches." These form at the foot of the sea wall; they are at a higher level than the mud in front of them, and as the sea retreats are left above spring tide high-water mark. As a result the sand in course of time is leached. The surface of these higher beaches then becomes covered with a mat of *Fimbristylis spathacea*, over which run the straggling shoots of *Ipomoea biloba*. A few other grasses and sedges are to be found scattered on these ridges, including a fair amount of *Stenotaphrum secundatum*. Here and there a small bush of *Jatropha urens* may be seen. In depressions which form at the foot of the sea wall, and collect rain water, *Fimbristylis spathacea* gives way to *F. diphylla*, and the aquatic grasses *Sporobolus virginicus* and *Paspalum distichum* occur, the latter being more prevalent where the water is least brackish. Cattle graze on these areas, and keep the grasses and sedges close-cropped.

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[1] From one point on the sea wall in 1929 the sea was plainly visible over a stretch of foreshore covered with *Spartina* and scattered mangrove seedlings. At the time of writing, some three years later, a belt of mangrove, 15–20 ft. high, growing on the mud bank about 80 yards from the sea wall—a lagoon intervening—completely cuts off all view of the sea.

The "lagoons." These vary from large areas, 50 yards or more in width, between the mud bank and the sea wall, to small isolated patches. At high tide they may resemble true lagoons—but as the mud bank in front of them enlarges, they are left dry except by the spring "flood" tides. They are distinguishable at once by their bare appearance. The *Spartina* does not encroach on them, the mixture of mud and sand probably proving unsuited to penetration by the stolons: the surface quickly dries and cakes in the sun between tides, and the saline nature of the soil prevents the plants of the higher sandy beaches from spreading on to them. Finally, such plants as do become established, are liable to be grazed by cattle. On these bare places are to be found, spreading thinly, creeping stems of *Sesuvium portulacastrum* and scattered patches of *Sporobolus virginicus*. A few clumps of *Batis maritima* occur here and there, and isolated plants of *Avicennia nitida*, closely cropped.

On the landward side, if the level rises sharply, the change in vegetation is abrupt, a line of drift débris separating the bare lagoon from the sedge-covered "beach." To seaward, however, a more gradual transition takes place, clumps of *Sporobolus virginicus* intermingling with the *Spartina* for some distance out on the soft mud.

The relations of the above-described constituents of the foreshore association are shown in the accompanying diagrammatic transect (Fig. 1), depicting a section of the shore where each society and habitat is represented. The following figures give an idea of the difference in soil constitution in the three types of habitat[1]:

		% of sand	% of salts
Sandy beach	Topsoil	88·7	0·082
	Subsoil	87·2	0·068
"Lagoon"	Topsoil*	61·7	0·986
	Subsoil†	86·0	0·645
Mud bank, composite sample		5·9	1·351

* Quantity of fine shell fragments removed before analysis.
† Large quantity of fine shell fragments removed before analysis.

THE *SPARTINA* SOCIETY.

Comparison with Spartina Townsendii. The part played by *S. brasiliensis* in the primary colonisation of the newly raised mud bank is of interest for two reasons. In the first place, the appearance of a grass in this rôle would appear to be unusual in the tropics, where muddy foreshores are more usually colonised directly by "mangrove." In the second place, its similarity in function and adaptability to *S. Townsendii* of European waters is striking. Its rooting system and power of extension by means of stolons render it eminently suited to rapid growth in soft mud and, like its relative, it is able to withstand several hours' submergence. Perhaps not unnaturally, owing to its superficial resemblance to the crop, *S. brasiliensis* is also known locally as "Rice Grass" or "Wild Rice." There is one very noticeable difference from *S. Townsendii*, however, in that the leaves of *S. brasiliensis* are somewhat coarse and stiff and terminate in sharp needle-like points that make walking barefoot through the grass a painful business. Perhaps it is partly on this account that, although cattle do graze on it, the local grass is not so palatable as *S. Townsendii* appears to be. In addition, the softness of the mud, where *Spartina* grows thickest, also prevents it being grazed to any extent.

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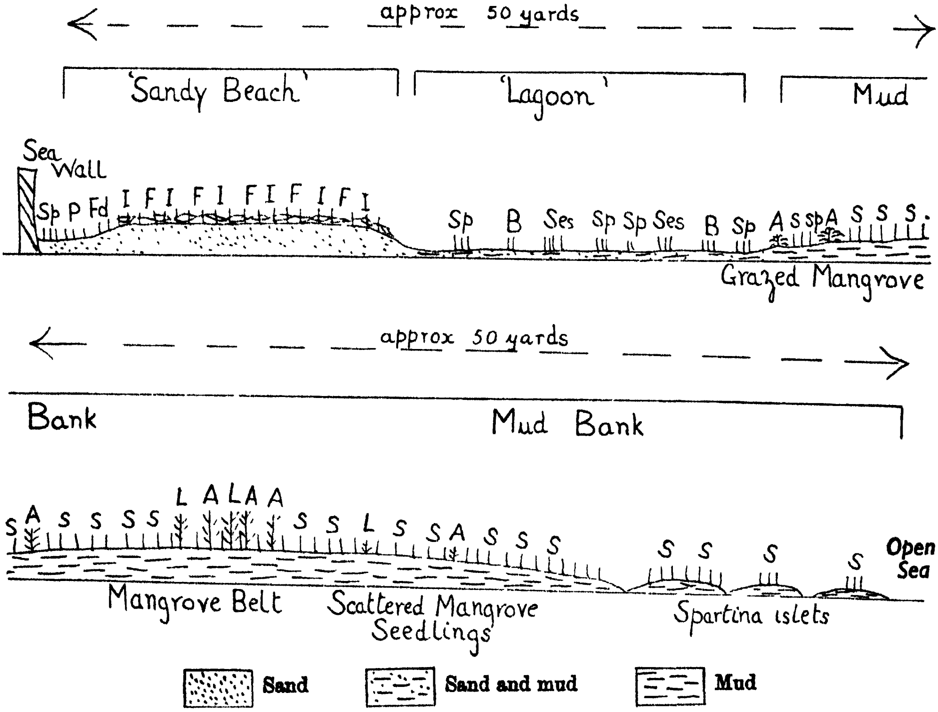
[1] I am indebted to Mr C. L. C. Bourne, Assistant Chemist, Department of Agriculture, British Guiana, for these figures.



A = *Avicennia nitida*; *B* = *Batis maritima*; *F* = *Fimbristylis spathacea*; *Fd* = *Fimbristylis diphylla*; *I* = *Ipomoea biloba*; *L* = *Laguncularia racemosa*; *P* = *Paspalum distichum*; *S* = *Spartina brasiliensis*; *Ses* = *Sesuvium portulacastrum*; *Sp* = *Sporobolus virginicus*.

FIG. 1. Transect 100 yards long from sea wall to open sea, showing belts of vegetation.

History of the development of the society. From an examination of earlier records of *S. brasiliensis* in the colony, it would appear to have been found originally on the banks of the Demerara River, near the mouth. Its mud-binding qualities in this locality were noticed at the beginning of the present century by a sugar planter who planted some of the grass on the muddy foreshore opposite an estate on the coast, east of Georgetown. There is a record of the grass extending for some 400 yards or so along the foreshore at this spot in 1908[1]. Subsequently, in 1915, erosion was taking place very rapidly on this part of the coast, and attempts were made to stay its course by the planting of various mud-binding species. One who assisted in these operations states definitely that the "Rice grass" was not to be found on this portion of the coast at the time. The sea was then seriously threatening the sea wall, and it is probable that the *Spartina* had been washed away. In order to check the sea's action, groynes were built to encourage silting, which has as a result continued steadily from about 1918 to the present day. At the same time, fresh plants of *S. brasiliensis* were obtained from the Demerara River and set out on the foreshore. From these beginnings the present large areas of the grass have arisen.

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[1] *Journal of the Board of Agriculture, British Guiana*, **1**, 3, p. 5, 1908.

Experiments with S. Townsendii. A year or two ago, some plants of *S. Townsendii* were obtained from England for trial under local conditions. On arrival, they were divided into three lots and planted:

(*a*) On a rather sandy area submerged at every tide.
(*b*) On a more muddy "lagoon" area, only covered by spring tides.
(*c*) On a bare patch out on the mud bank, covered by every tide.

The plants on the sand soon died. Those on the second area survived for a year or more, but never became properly established, and were finally smothered under a pile of drift débris. But the eight plants originally put out on the soft mud on a plot about 6 × 6 ft. have grown and spread so that the whole plot is covered with a thick mat of the grass, which is also spreading outwards. (One Courida seedling is to be observed in the centre of the plot.) The close-cropped condition of the *S. Townsendii* suggests that goats have been able to reach the plot at certain states of the tide, and have found this grass much more palatable than the local species. It would appear, therefore, that there may be possibilities for *S. Townsendii* on tropical shores in South America.

SUMMARY.

A short account is given of the coast of British Guiana, the main types of vegetation encountered there, and the modifications due to man's activities.

The rapid formation of new areas of foreshore as a result of silting is described, and an account given of the types of vegetation encountered thereon. The part played by *Spartina brasiliensis* in the primary colonisation of the newly raised mud bank is stressed, and this grass is compared with *S. Townsendii*. Mention is made of an attempt to establish *S. Townsendii* locally, and of the results obtained.

ACKNOWLEDGMENTS.

My thanks are due to Mr L. E. Codd and Mr C. L. C. Bourne of the Department of Agriculture, British Guiana, for assistance with the photographs and for partial analyses of the soils of the foreshore respectively. I am also indebted to Prof. F. W. Oliver for kindly sending me a quantity of literature on *Spartina* which would not otherwise have been available to me.

VEGETATION FORMULAE[1]

By L. DUDLEY STAMP, B.A., D.Sc.,

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INTRODUCTION.

THE value of a floral formula has long been recognised as indicating in the briefest possible space the essential characters of a flower, and as enabling a comparison or contrast to be made at a glance between two or more species. A family exhibits a definite range of floral formulae, yet the formula does not obviate the necessity for a detailed description of individual species.

The present paper has been prepared to suggest the desirability of establishing the use of vegetation formulae. A vegetation formula is designed to serve as a shorthand description in a standard form of a type of vegetation, just as a floral formula serves for a flower. Its value lies in the precision which it gives to the description of vegetation types, and especially in the way in which it will indicate affinities between related types of vegetation in whatever part of the world they may occur. At the present time the personal factor inevitably enters largely not only into the description of vegetation but also into the interpretation of descriptions. It is scarcely too much to say that each field ecologist is his own authority in deciding the form which his descriptions shall take, and very largely, too, in deciding the name under which he shall describe a certain type of vegetation. When the present writer was making a detailed study of the vegetation of Burma[2], he described types of vegetation ranging from evergreen rain forest, through deciduous monsoon forest, scrub forest, scrub with grassy undergrowth, to semi-desert. Two types in particular may be mentioned, namely, the *Acacia* thorn forest and the *Acacia* scrub, in which the dominant is *Acacia catechu.* Both of these types are very widespread in India and Burma and the monsoon countries generally. It was a little disconcerting when the writer afterwards paid an extended visit to Australia to find an extraordinarily close resemblance to many types of vegetation in that continent, more especially those usually referred to as mulga scrub and mallee scrub in South and Western Australia. Similarly the *Acacia* scrub of India with its rich undergrowth of grass is practically indistinguishable from many types of bush veld or savanna of such parts of Africa as Southern Rhodesia. The description of these different types of vegetation in the three continents of Asia, Australia and Africa, together with the very different names which have been given to them, would probably not indicate the close affinity which would be brought out at once by a vegetation formula.

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[1] Summary of paper presented to the International Botanical Congress, Cambridge, 1930.

[2] See **L. D. Stamp,** *The Vegetation of Burma.* Calcutta: Thacker, Spink and Co., 1925.

It is essential that the formula be kept as simple as possible, so that it may be used by travellers and explorers with only a limited knowledge of botany; but at the same time it may be so framed that it can give the greatest precision when applied by the professional botanist. It is recognised, of course, that a vegetation formula can never have quite the same exact meaning as a floral formula and that it must be based on the examination of sample plots or sample areas. That it will, however, result in greater precision and a better standardisation of descriptions than are available at present is indicated by the fact that it is almost impossible to draw up even a skeleton formula for descriptions already in existence. The writer, for example, finds that, despite the fact that he was working for five years on the study of the vegetation types of Burma, he cannot from his own notes and descriptions draw up adequate vegetation formulae such as are now proposed. On the other hand, where the traveller has not the time to carry out a detailed enumeration of sample plots and establish his formulae on the spot, this could be done, at least in outline, from carefully selected and carefully scaled photographs. The writer has attempted to test the feasibility of the formulae now proposed by taking a series of photographs of open forest or sparse scrub from a moving train, and has found it possible to work out an outline formula even from such photographs.

BASIS OF FORMULAE.

The formula proposed depends upon two separate considerations: (*a*) the enumeration of plants over a definite standard area; (*b*) the recognition of four or five main groups of plants for this purpose.

The standard area. It is proposed that one hectare be taken as a standard area, though of course the enumeration may be carried out over an area of any size and the results reduced to the standard area. Thus a hectare is equivalent to 2·47 or roughly 2½ acres and is equal to 10,000 square metres, so that the enumeration of small plants may be made on the basis of a square metre. The idea of a sample plot is by no means new. It has long been the custom of forest officers to study their forests on the basis of sample plots, and of ecologists to base their descriptions on similar plots. For the purpose of a vegetation formula it is merely necessary that enumeration carried out over sample plots, which may be of any size whatsoever, shall be reduced to the standard area. It may be thought that the standard area suggested is too large. It is, however, necessary to bear in mind the very varied types of vegetation which must be covered. One has tropical forests, in which there may be but one or two individuals of a particular species even in a hectare of dense growth, whilst in semi-desert types individuals become widely scattered.

Main groups of plants. It is suggested that for practical purposes types of plants to be enumerated should be considered as divisible into five broad groups[1]:

Trees (A, from the Latin *arbor*).
Shrubs (F, from the Latin *frutex*).
Herbaceous plants (H, from the Latin *herba*).
Grass (G, from the Latin *gramen*).
Cryptogams (C).

It is recognised that *herba* is not a very satisfactory word, but its use in the sense proposed for herbs, excluding grass, is already widespread in the adjective "herbaceous." The basal vegetation formula thus becomes:

$$xA+yF+zH+uG+vC,$$

where x, y, z, u and v are the numbers of individuals per hectare. Since there are 10,000 square metres in a hectare and H, G and C will be normally enumerated over 1 square metre, this formula will be more simply

$$zA+yF+10^4\,(zH+uG+vC).$$

An alternative method of arranging the formula will be considered in the Appendix.

ELABORATION OF FORMULAE.

The initial observations which are absolutely necessary for the drawing up of even a simple formula are as follows:

(1) The number of trees and shrubs and other principal members of the vegetation per unit area.

(2) The approximate or average height of the members of each group.

(3) The dominants of each group.

Such main features of the vegetation can be observed even by a traveller passing rapidly through a country. Just by pacing out, for example, a rough area during, let us say, an hour's halt on the march, he would be able to know the number of trees, their approximate height, their general character, together with the type of undergrowth, whether woody, herbaceous or grass, and would be able to produce a rough formula of the nature of

$$150A\ (30)+300F\ (2)+\infty G.$$

This is obviously the formula for an open type of forest, the trees being 30 metres high, there being about 150 to the hectare, with an undergrowth consisting of fairly numerous shrubs about 2 metres high, and a large proportion of grass. Such is the simplest type of formula which can be produced; but even so it introduces a definite element of precision, namely, that there is a certain number of trees in a certain area, and that those trees reach an average height as definitely stated. Also that the undergrowth is definitely of a mixed character of shrubs and grass, the grass being present in abundance.

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[1] Climbers may be grouped as F or H according to their character, their height in metres will be equivalent to that of the trees and their dependence may be shown thus $\overparen{A+F}$.

Even to the untrained observer certain refinements in this rough formula may be readily introduced:

(*a*) For trees and shrubs the presence of more than one storey may be indicated by duplicating the symbol: $A+A'$, and $F+F'$.

(*b*) The general character of the trees or shrubs may be indicated by suffixes such as: *s* (sempervirens or evergreen), *d* (deciduous), *c* (coniferous).

(*c*) The average height of the vegetation is of course important and should be expressed in metres, the figure being placed in brackets after the group to which it refers.

(*d*) For all types of vegetation the letters *a*, *b*, *c*, *d*, etc., may be used to indicate dominants: *x*, *y*, *z*, etc., to indicate the absence of dominants or the presence of numerous species. The relative importance of the dominants may be expressed by the order, viz. *acb*, whilst a species important but relatively subordinate may be marked by underlining, thus $ab\underline{d}$.

Thus the same type of forest as indicated in the formula already given may be more elaborately described as follows:

$$150A^d ab\,(30)+300F^s cF^d d\,(2)+\infty Gx.$$

It will be seen that such a formula indicates the existence in this particular case of two co-dominants amongst the trees, *a* and *b* (their relative abundance being expressed by the order *ab*). The traveller, whilst not knowing the species of tree, can express this important fact, leaving it to the botanist to determine the identity of *a* and *b*.

CONCLUSION.

If the principle of vegetation formulae is acceptable to ecologists, numerous refinements and extensions will be necessary, but the present outline scheme is put forward with the hope that it may induce a greater precision of description by travellers. It is to be noted that the formula is at least partially complete without the naming of the constituent species.

APPENDIX.

An example of a formula based on a sample plot.

A typical plot 25 by 25 m. was selected in a *Pinus-Picea-Betula* forest (damp *Myrtillus* type approaching *Oxalis-Myrtillus* type of Cajander) on the island of Sayneensalo, near Kuopio, Finland. With the expert help of Mr Henry J. Howard of the Museum, Norwich, and a number of assistants, the following enumeration of trees and shrubs was made:

a. *Pinus sylvestris* (Scots pine), 20 large (25–30 m.), 4 small (15–25 m.), 2 seedlings.
b. *Picea excelsa* (Norway spruce), 19 (25–30 m.).
c. *Betula verrucosa* (Birch), 13 (15–25 m.).
d. *Juniperus communis*, 72 (0·50–2 m.).
e. *Alnus glutinosa* and *A. incana*, 147 bushes (0·50–2 m.).
Sorbus aucuparia (Mountain ash), a few small seedlings.
m. *Vaccinium myrtillus* (*Myrtillus nigra*) (Bilberry), abundant.
n. *Vaccinium vitis idaea* (Cowberry), abundant.
l. *Linnaea borealis*, locally abundant.
Oxalis acetosella, locally abundant.
Maianthemum bifolium, abundant.
Trientalis europaeus, very common.
Fragaria vesca, very common.
Viola canina, common.
Geranium sylvaticum, common.
l. *Pyrola rotundifolia*, frequent.
P. minor, frequent.
Pteris aquilina, frequent.
Phegopteris dryopteris, sporadic.
Lycopodium clavatum, local.
Lichenes (λ), not abundant.
Musci (μ), abundant.

For the study of the ground flora two sample plots of a square metre each were chosen. Counts showed respectively 124 and 196 small shrubs (*Vaccinium* and *Linnaea*) per square metre, and about the same numbers of smaller herbaceous plants. For the purposes of constructing a formula, these have been averaged at 150 to the square metre. The fully grown trees in this forest average about 25–30 metres high; the annual rings in a number of stumps were counted and showed an age of 75 to 120 years. From the above details it will be found that the formula for this forest is

$$900A^{cd}abc\,(15\text{-}30)+3000F^{ds}ed+10^4\,[150F'mn\underline{l}+150Hx+\infty C\mu\lambda].$$

The letters *a*, *b*, *c*, etc. refer to the above list.

THE WILLOWS OF THE WESTERN PART OF THE ISLE OF WIGHT

BY L. H. DUDLEY BUXTON, M.A., D.Sc.

AT the suggestion of Dr Burtt Davy[1] I made a survey of the willows in the region between Freshwater and the Needles in July and collected specimens for the herbarium of the Imperial Forestry Institute at Oxford. It may be noted that my own special interest is the relation of the "natural" vegetation to man. The region may first be divided into a chalk ridge rising to over 500 ft. and culminating in the Needles. This ridge is bounded on the south by high cliffs overlooking the Channel, and although in hollows it contains such shrubs as elders and privets is practically devoid of willows, probably owing rather to the absence of shelter than to the nature of the soil. North of this lies a region of recent sands and clays, rising once more to cliffs on the north. The trough is occupied by cultivated land, the cliff top, where not built on, is mostly gorse or heather, while the clay surface of the undercliff, owing to its unstable nature, is (apart from a small area) more or less unaffected by man; it has a very rich and varied flora. The dominant species of willow over all the clay belt is *Salix atrocinerea* Brot.[2] which is found very frequently in the hedgerows and on the cliff top, and together with brambles grows in profusion in dense brakes on the undercliff, reaching a height, when undisturbed, of nearly 20 ft. Species of *Prunus* grow on the drier parts of the undercliff, otherwise willows are the only shrubs here. In the cultivated region, though not very frequently, *S. fragilis* × *alba* is found in hedgerows, and there are two noble trees of a hybrid of this type at the foot of the downs, in a farmyard: otherwise all the willows I found were shrubs. Only one bush of true *S. fragilis* L. was found. In the same region a bush of *S. viminalis* L. and a hybrid *S. purpurea* × *viminalis* was found. I think, subject to correction, that it is the twigs of this species that are widely used in the island for lobster pots. In addition to *S. atrocinerea* Brot., the undercliff contained a solitary bush of *S. incana* Schrank., though how it came to the inaccessible spot where I found it, is uncertain. *S. aurita* L. also grew there, though not in profusion, and apparently hybridised with *S. atrocinerea* Brot., while a solitary bush of *S. caprea* L. occurred amongst gorse on the cliff top. Pending further expert work on the willows it is of interest to note that all the three common varieties of *S. atrocinerea* Brot. occurred, the one with dusky undersides to the leaves, one with a green glabrous underside, and a tomentose variety. In conclusion it should be noted that while *S. atrocinerea* Brot. was everywhere, whether in cultivated or "wild" regions, the *S. fragilis* × *alba* and the *S. viminalis* L. group occurred only in cultivated regions. The remaining species were not sufficiently common to make any generalisation.

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[1] I have to acknowledge with gratitude the constant advice and assistance of Dr Burtt Davy and of Mr Beak who identified my specimens.

[2] This is the sallow which has, until recently, been known in this country as *S. cinerea* L. True *S. cinerea* L. has not been found in Britain.

A SUPPLEMENTARY NOTE ON "A SUGGESTED EXPLANATION OF THE PREVALENCE OF VIVIPARY ON THE SEA-SHORE"

BY A. C. JOSHI.

IN the writer's earlier paper entitled "A suggested explanation of the prevalence of vivipary on the seashore," published in vol. XXI of this JOURNAL, a statement was made on p. 211 that "rains make no difference there (in the mangrove swamp) and the salt content of the soil remains high and approximately uniform throughout the year." When making this statement I had no access to any published paper on the subject but simply wrote what appeared to me as most probable. In a letter, however, Prof. F. W. Oliver, F.R.S., of the Egyptian University, Cairo, tells me that this statement needs modification. He writes: "From 1904 to 1909, I took ecological parties to investigate the conditions of a salt marsh in Brittany (the Bouche d'Erquy) and there made many series of determinations bearing on this point. The soil water of a salt marsh when the tide runs off is roughly speaking the strength of sea water, say 3 per cent. solution of salts. But this is liable to immense fluctuations. (1) Take the case of the last of the higher tides. The ground will receive no further visitation of sea water over the period of the neaps, it may be for a period of 5 or 6 days. With strong insolation and evaporation, we often found the initial 3 per cent. to rise to 6 or even 9 per cent. salt in that period. When the spring tide returned the excess would be washed out. (2) In the case of heavy rainfall towards the close of the period of neaps, soil containing a solution of 6 or 8 per cent. would be reduced in 12 hours' rain to half or less than half that concentration. The effect is especially noticeable in salt marsh soils containing a good deal of sand and being in consequence readily permeable to rainfall."

There is nothing, however, in Oliver's records to show that the water of the salt marsh ever reaches a dilution much lower than that of sea water or anywhere near the condition found in inland saline soils after a strong downpour of rain, which is very near the condition of ordinary soils. Nor is there at present evidence which shows that this diluted condition of the water of the salt marsh ever lasts for a sufficiently long period during which seeds can germinate and new plants can fully establish themselves.

In the end, even if it is demonstrated by someone that at certain times the salt marsh has got a very low concentration of salts and this condition lasts for a sufficiently long period during which seeds can germinate, it is also necessary to show that the seeds of the mangrove plants mature just during this period in order to disprove the explanation advanced by me, for inland saline soils and seashore swamps differ greatly with regard to the fate of the seeds when these happen to fall into them during the time of high salt concentration. Inland saline soils are usually dry when their salt concentration is highest, and if any seeds happen to fall into them at this time, owing to the absence of water, no salt will permeate these seeds which will therefore remain free from injury and perfectly viable unless it be for some other reason. These seeds will simply lie dormant, and whenever the next rain comes they can germinate and grow into new plants. A different fate, however, meets the seeds falling into the mangrove swamp when its salt concentration is high as is usually the case. The seed will be soon injured and become unviable. Even if the concentration of the salt is diluted at a later date by heavy rain, they will not be able to germinate.

For these reasons there are no grounds at present to change the views put forward by the writer in his earlier paper.

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THE MYCORRHIZA OF CONIFERS: A REVIEW

By M. C. RAYNER.

PRODUCTIVE research on the problems associated with the mycorrhizal habit in trees has reached a stage demanding from the investigator not only the use of modern experimental methods but also a definite point of view respecting the precise nature of these problems.

In certain groups of plants the application of pure culture methods to similar problems has demonstrated the existence of mutualistic relations of great importance in the economy of the hosts, and it is evident that the older theories respecting the nutrition of mycotrophic plants in general require revision in the light of modern work.

The case of trees is of special interest because of the large and heterogeneous group of species represented by the vascular hosts, and the practical importance of the habit in relation to tree nutrition and growth. The controversial atmosphere that has enveloped the subject since Frank's discovery of tree mycorrhiza in 1881, and his subsequent publication of a novel theory of nutrition—at once repudiated by Hartig and other contemporary plant pathologists—can be dispersed only by evidence based on rigidly controlled experiments and the accumulation of data designed to test the validity of definite hypotheses.

These reflections are provoked by a study of two recent publications on the subject, one by E. V. Laing (**1**) including a section dealing with "Mycorrhiza in Conifers," the other by R. E. McArdle (**2**) entitled "The relations of mycorrhizae to Conifer seedlings." Both contain observations of interest to botanists as well as to foresters. Plant physiologists and ecologists should welcome Laing's observations on the correlation of mycorrhiza formation with the differential water-holding and oxidising properties of peat soils, as well as the record of increased oxidative activity of peat associated with promotion of mycorrhiza formation, following upon the addition of substances such as magnesium carbonate.

Evidence bearing on changes in the soil solution in contact with fungus roots is of particular interest to the student of mycotrophic nutrition. It is therefore worthy of note that whereas Laing states that he has observed no direct correlation between "the absence and presence of mineral bases in the peat solution and the formation of mycorrhiza" (*loc. cit.* p. 28), in a later section (p. 33), he records experimental evidence that contact with mycorrhiza "can increase the quantity of mineral bases in solution in certain peat soils." The latter observation is extremely significant and important.

The methods used successfully by McArdle for promoting mycorrhiza formation in artificial cultures merit attention. To describe the latter as "pure cultures" is, however, misleading. This designation should be reserved for cultures grown under absolutely controlled conditions uncontaminated by any organism other than those introduced during the experiment.

Neither author contributes anything towards a final solution of the historic controversy respecting the physiological relations between the root fungi and their hosts. Laing concludes, with so many of his predecessors, that the relation of mycorrhiza with Conifer nutrition is "an open question." "Evidence has been advanced in support of both views!" In a later paragraph, however, he makes the extremely pertinent statement that "the question of mycorrhiza formation and the parasitic or non-parasitic tendencies of the fungi concerned is largely one of soil improvement," without apparently realising the direct relevancy of this to his main conclusion.

An important contribution to this aspect of the subject has recently been summarised in the final report of a Research Committee of the British Association for the Advancement of Science (**3**).

McArdle likewise was able to obtain "no conclusive proof...that the presence of mycorrhizae on the roots of seedlings is either helpful or harmful to the seedlings."

It is not proposed to anticipate here the forthcoming publication of an experimental study of the genus *Pinus* which has yielded positive evidence pointing to an entirely different conclusion. In both the papers under review, however, certain implicit assumptions respecting tree mycorrhiza appear to me to be erroneous and misleading, making it practically impossible to interpret observations on field material such as that described and figured. It is believed that similar assumptions by other observers have been responsible for much needless controversy respecting the physiological relations between fungus and host in trees, have led to confusion in the literature, and have greatly retarded the progress of research.

Let us examine these assumptions. Both McArdle and Laing apparently believe that the "mycorrhiza" formed by Conifers exotic in the United States and Great Britain respectively is normal for the species, showing similar physiological relations and playing the same rôle in nutrition as those associations formed in their native habitats.

For example, McArdle figures the mycorrhiza formed by Norway Spruce in Michigan, describing it simply as "mycorrhizae on Norway Spruce, suspected of being formed by *Cortinarius argentatus*." This mycorrhiza shows more or less profuse intracellular infection of a casual kind in the cortical cells, but is not of typical ectendotrophic structure and suggests an unbalanced relation between mycelium and root.

Laing makes similar assumptions in respect to *Pinus montana*, *Picea excelsa*, *Larix decidua*, *Thuja plicata* and *Abies grandis* growing in Great Britain. Mycorrhiza of Mountain Pine is figured showing intracellular penetrations of the cortical tissues of the root by mycelium (*loc. cit.* Pl. IV, figs. 2, 3).

That of Silver Fir illustrates "destruction of cortical cells" and exhibits profuse intracellular penetration very unlike that in typical endotrophic infection.

Now, it is quite possible that the mycorrhizae formed by trees of these species growing in Scotland may result from associations with the same fungi as those responsible in their native habitats, or with others capable of forming a balanced relationship under existing conditions of soil and climate. It is significant, however, that "destruction of the roots by the fungus" recorded for Scots Pine on certain soils, is described in spruce as "much more complete than in pine" (*loc. cit.* Pl. IV, figs. 1, 2).

The known facts for these coniferous species are as follows:

All, with the exception of Silver Fir and *Thuja plicata*, have been proved experimentally to form multiple mycorrhizas with a number of fungus species, and it may be regarded as almost certain that Silver Fir has the same habit. Moreover, Melin's researches in Sweden have shown that different root fungi are associated with Scots Pine, Norway Spruce, and Mountain Pine in different localities and soils (**4**, **5**). Some, but not all, of these fungi have been identified with woodland species of Hymenomycetes, the sporophores of which are commonly associated with the trees. There is, therefore, direct evidence on which to base the hypothesis that the formation of normal and functional mycorrhiza by these Conifers is very delicately attuned to local conditions and is best satisfied with specific fungi or fungus strains in different localities.

It does not follow, therefore, that "mycorrhiza" observed in a particular nursery or plantation away from natural stands of the tree is necessarily either morphologically or physiologically identical with any type of associations formed by the hosts at any native station, or indeed that it represents a "balanced" type of association at all.

Let us now turn to the possibilities of error within the limits of a single native species, e.g. Scots Pine, *Pinus silvestris*. It is already clear from published researches that the formation of healthy and normal mycorrhiza in general is determined at any given moment not merely by proximity of the appropriate mycelium but by the physiological condition of both roots and hyphae. The quality in the latter that Melin has called "virulence" is not yet susceptible of accurate definition, but its acceptance involves recognition of a particular physiological condition in the mycelium as an essential factor in mycorrhiza formation (**5**, **6**). Moreover, it is known that if these conditions are not fulfilled or *if they are temporarily upset experimentally*, normal mycorrhiza is replaced by an abnormal association described as "pseudomycorrhiza."

The term "pseudomycorrhiza" as at present used covers associations of several distinct kinds occurring naturally or induced experimentally. Some are formed by parasitic or quasi-parasitic soil fungi, others by the inversion of a balance normally maintained when the fungus associate is a recognised mycorrhiza-former, and yet others by parasitic attack on a normal mycorrhiza by other soil micro-organisms. Melin isolated and identified two soil fungi specially concerned in the formation of pseudomycorrhiza in Swedish soils, and identical structures and relations have been observed both in the United States and in Great Britain. Sometimes pseudomycorrhizas bear a more or less close external resemblance to true mycorrhizas, sometimes they change their character with continued growth and acquire the external and structural features of true mycorrhizas; the latter are especially common in certain nurseries, and in seedlings of pine often look like forked mycorrhizas borne terminally upon rather slender rootlets—the slender region constituting the pseudomycorrhizal part of the structure. Sometimes they are easily recognised by external characters only, if the observer has a detailed acquaintance with the types of normal mycorrhiza to be expected for the host tree. *Always they show abnormal structural features when sectioned and examined microscopically, and are associated with poor growth and impaired vitality in the host.*

The presence of intracellular infection in the cortical cells is not in itself sufficient to identify pseudomycorrhiza, or even to prove a parasitic tendency in the fungus partner, because ectendotrophic structure is a normal feature of the mycorrhizas of certain trees. On the other hand, heavy intracellular infection without evidence of subsequent digestion of the mycelium should be viewed with suspicion and subjected to careful comparative scrutiny before it is accepted as a structural feature of mycorrhizas normal for thrifty trees of the species under consideration. It is suggested that microscopic examination of the Pine mycorrhiza (Pl. I, fig. 4) and of those of Silver Fir (Pl. IV, fig. 2), figured by Laing, might be of interest from this point of view.

It is probable that many evolutionary stages marked by greater or less specialisation of the symbiotic relations are represented among trees. In the genus *Pinus*, I have reached the view that the association is highly specialised and depends upon soil conditions for maintenance of the normal equilibrium. Any disturbance of these conditions may result in changes that react adversely or even disastrously upon the health and vigour of the host.

For correct interpretation of field observations it is so important that the point of view of the investigator should be clearly defined that I venture to summarise certain of my own conclusions for the genus *Pinus* based on field observations on a number of species in various parts of Great Britain and Europe, in the Eastern United States of America and, in the case of one species, *P. ponderosa*, in the mountains of South California; and on experimental observations on field plots and pot cultures of a more limited number of species in the south of England.

(*a*) The conversion of a large proportion of the sub-lateral root system into mycorrhizae is a natural and inevitable habit in the pines studied, and the formation of healthy and functional mycorrhiza may be regarded as a normal condition for normal nutrition and growth under woodland conditions, there being a direct causal relation between healthy mycorrhiza and thrifty growth (Rayner (**6**)).

(*b*) Under stabilised conditions the association of fungus and host in pines is a balanced one, closely correlated with local conditions of soil and often operating within very narrow limits. A number of such associations may be formed according to the range of the species, differing in respect to the identity of the fungus associates and the precise character of the physiological balance. Some of these may be interchangeable in different situations; others are more specialised, and, if disturbed or replaced by others, may cause marked interference with vigour and growth. Similar considerations apply to environmental factors such as those brought about by changes in the humus layer in old woodlands, and such changes may react unfavourably on the trees.

(*c*) The first step in a study of the mycorrhiza of any Conifer is the adoption of a standard of comparison by observations on the external and internal structure of mycorrhizas from as large a range of *natural* stands as possible. Evidence should also be collected concerning the mycorrhizal behaviour of seedlings when exposed to non-woodland conditions more or less distant from native stands of the species. Interpretation of the behaviour of such mycorrhizas as the latter can be judged only on a basis of comparison with those from native stands. Mycorrhizas formed by seedlings or young trees showing checked growth should receive special attention in view of the possible replacement of normal mycorrhiza by pseudomycorrhizas of various types. The association of the latter with different and specific soil conditions should be carefully noted.

It is believed that such comparative field and laboratory observations are an essential preliminary to experimental studies designed to test the physiological significance of mycorrhiza in any given species of pine.

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LETTER TO THE EDITOR

VEGETATION SUCCESSION AND REGIONAL SURVEYS, WITH SPECIAL REFERENCE TO TROPICAL AFRICA

To The Editor of *The Journal of Ecology*.

Sir,

Following on the fairly recent recognition in temperate countries of the dynamic aspect of vegetation, it has become the custom of many ecologists to describe all the types of vegetation in an area as related by succession to one or a few climax types. I wish to suggest that the idea of large-scale succession of vegetation is being used to a degree which is not justified and is sometimes leading to definitely wrong conclusions.

The word succession is used to cover two distinct processes, inherent succession of vegetation and physiographic succession. The fundamental difference between the two ideas is this. In the former the vegetation is unstable and tends to change in *one* direction, even when all the factors of the environment, save those due to the vegetation itself, are constant. In the latter the vegetation is in a state of equilibrium with the environment. As the environment is liable to change in *any* direction, so corresponding changes take place in the vegetation.

The inherent succession of vegetation is the changes which take place through the plants altering their own environment. I, personally, would like to confine the use of the word, succession, to this sense. The following are a few examples of intrinsic succession in natural vegetation: the development of mesophytic woodland from swamp in temperate countries through the upward growth of peat, the formation of complex plant cushions in Arctic fjaeldmark, the stabilisation of dunes and screes, the dependence of epiphytes and creepers on their supporting plants and the relations of many of the African Capparidaceous shrubs to the other species under whose shelter they grow. In natural vegetation this kind of succession is important mainly in determining the details within the main types, whose regional distribution is ordered by other means. The stages in the reversion of the plant covering of areas cleared of their natural vegetation are also true, or intrinsic, vegetational succession.

In order to demonstrate my point, that alterations in vegetation due to physiographic changes should not be described as true succession like that just discussed, I will refer to tropical Africa and to a recent paper by Phillips (**1**). (This paper is not mentioned in order to single it out for criticism; it is quoted as one example of many using the principles under discussion, because it has already become widely known, owing to the excellence of its descriptive part.) Phillips describes many types of vegetation in the area with which he deals and then, incidentally without giving his evidence, links them all up in successional chains. Many of his types are soil types, while others may be modifications due to fire or other causes. Other authors, such as Snowden (**2**), have followed Phillips in linking up different soil types in one successional line.

Not being familiar with the area described by Phillips, I will not attempt to refute any of his actual examples. Instead I will quote three comparable cases of changes in vegetation from other parts of the continent.

In parts of the Sudan there are isolated groves of Date Palms growing in wadies. Owing to lessening of the underground water supply some of these groves are dying off and are tending to be replaced by thorn scrub. Some ecologists might describe this as succession from palm grove to thorn scrub. This "succession" is quite different from the inherent kind, for it depends entirely on an external factor. Only a study of the water supply can determine whether the water is merely shifting over to the other sides of the wadies and may return and reverse the change, or if the source of the water is drying up, and, if so, why.

The second example is from the great Tanganyika Plateau of Northern Rhodesia. Some of the streams have reached their base levels near the edge of the plateau and have formed small plains. These plains have heavy, badly drained soils and are covered with grass. They correspond to the grass plains which Phillips asserts are stages in the development of woodland. They are separated by fringes of Combretaceous Bush from the *Brachystegia* Woodland which covers most of the plateau. The succession here is undoubtedly towards the grass plain vegetation, as the valleys become more and more filled up by deposition of silt from the river and by surface wash from the wooded, higher country around. Owing to the extensive rifting and faulting, which have occurred round the edges of the plateau in connection with the Great Rift Valley system, the streams have been rejuvenated where they flow off the edge. They are therefore cutting back into the flatter parts of their valleys above. As the rivers cut down, drainage and leaching of the valley floors occur, so that the Combretaceous Bush first tends to invade the grass and in turn to be replaced by *Brachystegia* Woodland. In describing the vegetation of such valleys in the stereotyped way, which, therefore, would one describe as the climax, grass plain or *Brachystegia* Woodland?

In much of Central Africa the existence of grass plains and of other waterlogged types of vegetation is bound up with the presence of laterite pans. When the causes of the formation of laterite are so much a matter of debate amongst experts, it is surely premature for the mere botanist to decide in which way a plant community dependent on laterite is changing. Probably in some cases lateritic places are drying up and becoming more wooded, while in others the tendency is for further formation of laterite and for the places to get wetter.

One of the most striking things about the vegetation of Africa is its dependence on soil factors, such as the ones just described. In the drier parts of the continent nearly all the variation in the vegetation of a district can be related to water supply. In moister parts each type of soil has its characteristic vegetation. The three examples given above show the radical difference between true succession and changes dependent on such factors. In the former the change is in one fixed direction and is a botanical problem. In the examples it is clear that the change may be in either direction, and that the direction is due to causes whose sphere is geographical, not botanical. In such cases the ecologist may rest content with discovering how the vegetation is correlated with the environment. If he wishes to study the changes in the environment itself, he must realise that this is not botany. He must not apply to a purely geographical study terms which are applicable only to ecology itself. The kind of factors used as examples are more obvious in Africa than in temperate countries, because of the flatness and uniformity of the country over enormous areas and the long time during which differentiation of the soils has been taking place. The principles argued out above, however, if true at all, must be of universal application. Even cases of the development of new soils, like the emergence of land from the sea, are often not true intrinsic succession, from which they are not distinguished by their describers. In these cases the development of the vegetation is obviously in one direction, but since physiographic successions may be reversible, it would seem better to treat such "successions" like the reversible ones. The changes in the vegetation should not be described as a succession, unless it can be proved that the plants of the early stages themselves cause changes which encourage the formation of the later stages. Although plants always alter their environment to some extent, in practice it is possible to distinguish between changes due to these alterations and those taking place in spite of them.

A thing which has done much to further this unsound belief in the universal succession of vegetation is the idea of the convergence of all the types of a region towards a mesophytic climax. From the observation that the colonisation of very wet and very dry habitats often goes by stages, becoming progressively more mesophytic, the false inference was made that all types in a region tend to converge. Africa shows clearly that, besides the admitted tendency of some types to converge, there is differentiation of soils and consequent divergence of those types of vegetation which are dependent on soil types. Even the drying of aquatic habitats by plants in all cases may be queried, for one effect of the plants is to impede drainage and so increase flooding.

In making a regional survey the following would seem to be the right course. After examining all the types of vegetation, it should first be decided what is the climax or natural vegetation of the region. This will not be a single type, as is commonly understood by the term climax, but a whole series of types. The types will mainly be determined by the physiographic factors discussed above, but in certain cases fire, biotic, and other factors may be important. These types are not successional stages. The second step is the study of the effect of artificial changes on this natural vegetation, and the next is that of the successions following on after these changes. This method involves an arbitrary distinction between the natural, or relatively stable, factors, which are all studied together, and the artificial, or relatively unstable, ones, which are studied separately. Ideally, each of the natural factors should be studied separately, as it reacts with each of the other factors, but actually this course is not possible. For instance, in studying the vegetation of a mountain the full effect of the variations of the climatic factors at different heights cannot be worked out on all the soil types, since these will not all occur at all heights. Bogs may not occur above a certain height or screes below another. In practice one has to make the arbitrary distinction, examine or reconstruct the "natural" or climax vegetation, and infer the separate effects of the different factors as well as one can from such combinations as do occur.

Criticism of the remarks made here would be welcome. To aid this the theoretical conclusions are summarised as follows:

(1) The radical difference between the changes that occur in vegetation entirely through its own action on the environment without changes in the external factors, and those due to changes in the environment irrespective of the action of the vegetation, seems to be insufficiently recognised by some ecologists. In the first case the vegetation is unstable and tends to change in one direction in spite of the constancy of the external factors. In the second it is in a state of equilibrium with the external factors and changes only as they change.

(2) It would seem advisable to use the word succession for the first kind only. If this is not now possible, owing to the word having been used for so long to cover both types of change, descriptions of vegetation should always make quite clear to which kind of change they refer.

(3) The vegetation of a region does not tend towards a single climax type, since differentiation, as well as convergence, of soil types is always taking place. The real climax, or "natural," vegetation is a whole series of types. These types are usually determined by factors of local climate and soil, but other factors may play a part.

(4) True intrinsic succession rarely occurs between the different types of natural vegetation. When it takes place on a large scale, it is usually the result of "artificial" changes. In the climax vegetation it generally occurs only on a small scale and determines the details within the main types.

Since Africa has been used to provide arguments for these views, the opportunity may be taken to make one or two suggestions about the study of the vegetation of the continent.

Shantz and Marbut have produced a general account and maps of the vegetation and soils of Africa (3). Though useful in drawing attention to the subject, this book is misleading in some ways, particularly with regard to the mapping of the soil types. Owing, no doubt, to the great age of many of them, there is far more difference between the different types of soil in any one area than there is between the characteristic soils of Shantz and Marbut's different soil regions. The soils of the continent can therefore hardly be mapped by choosing characteristic types, as these authors have attempted to do. The soil types, being determined by topography and history, as well as by climate, mostly have a fairly wide climatic range. The ranges of the various types overlap without their boundaries coinciding. The first step in studying their distribution would be to work out separately the geographical range of each soil type, such as laterite, "cotton soils" and blown desert sands. Then regions could be worked out and characterised, not by single types, but by lists of the types found in each.

With regard to the relations of the soils to the vegetation, a very useful piece of work would be to follow single soil types through the length and breadth of the continent and note the degree of constancy and change in the vegetation as different climatic zones were entered. Some interesting things might be discovered. For instance, I have noticed an extraordinary similarity in general appearance, genera and probably even species in the ground vegetation of the Kalahari Sand formation at Livingstone on the Zambezi and of a similar red sand at Lourenço Marques to that of the "goz" sands of the Sudan. Yet the former bear open forest of broad-leaved trees, while the latter are dominated by thorn scrub. Both the Kalahari Sand and the gozes are blown sands, but they are quite unconnected, for the former mark an ancient northward extension of the Kalahari Desert and the latter a southward one of the Sahara. Similarly it has been noticed that over-grazing of the tall grass covering the heavy, grey clays of the flats of the River Kafue in Northern Rhodesia allows colonisation by a variety of annuals reminiscent of the cotton soils of the Nile Valley.

A useful parallel study would be the single vegetation types in the same way. It would be found that soil preferences are not always constant in different climates. It is curious, for example, how the acacias, which are ubiquitous in the hot, dry parts, become more and more restricted to particular soils as the rainfall increases.

Another piece of work, which would be of wider interest than would appear at first sight, and which would supply useful clues for the study of the regional vegetation, would be an examination of the large anthills which abound through so much of Central Africa. These termite mounds not only usually bear vegetation different from the ground around, but those in different communities usually themselves have different plants. Many of the plants confined to anthills in one region are important parts of the general vegetation in another. For instance, amongst the bushes peculiar to anthills in North-Eastern Rhodesia, *Balanites aegyptiaca* and *Zizyphus mucronata* are abundant trees on the flat in the Sudan, while *Markhamia lanata* is common on the flat further south in Northern Rhodesia. In other cases anthill plants may grow on the flat in different plant communities in the same region. In North-Eastern Rhodesia *Acacia hebecladoides*, for example, is found in two main habitats, on anthills in *Brachystegia* Woodland and Combretaceous Bush, and on the flat on low-lying plains of white clay. Probably both habitats agree in having compact soil with much surface drainage and little penetration of water, resulting in waterlogging of the surface soil in the rains and drought in the winter. As a rule the anthill vegetation varies with the vegetation of the surrounding country, but sometimes an area may be found with anthill plants which usually grow in different surroundings. It is probable that in some of these cases the anthills bear relics of a vegetation which has been ousted by other types through such influences as the increase of fires, which often spare the anthills. For instance, there are in North-Eastern Rhodesia scattered areas of *Brachystegia* Woodland whose anthills are clothed with bushes typical of the dense semi-deciduous scrub of *Combretum*, *Grewia*, Capparidaceae, etc., which is known locally as *amateishi*, instead of the species usual on anthills in *Brachystegia* country.

REFERENCES.

(1) **Phillips, John.** "Some important vegetation communities in the Central Province of Tanganyika Territory." This JOURN. **18**, 193, 1930.

(2) **Snowden, J. D.** "A study in altitudinal zonation in South Kigezi and on Mounts Muhavura and Mgahinga, Uganda." This JOURN. **21**, 17, 1933.

(3) **Shantz, H. L.** and **Marbut, C. F.** "The vegetation and soils of Africa." *Amer. Geog. Soc. Res.* Series 13, 1923.

Yours faithfully,

A. P. G. MICHELMORE.

LUWINGU,
N. RHODESIA.
24/8/33.

[The extraordinarily varied nature of the natural and semi-natural vegetation of most parts of the earth's surface, and the extreme complexity of the processes involved in its determination and change, render its correct interpretation a slow and difficult task. Mr Michelmore is not the first student of vegetation to find current conceptions inadequate or misleading for his work. Criticism and analysis of the kind he offers are not only always welcome, they are indispensable to the advance of the subject. But it may be pertinently suggested that such criticism and analysis would be more valuable if they took the history and literature of the subject into account. The starting point of the more modern work on succession was Clements' *Plant Succession*, published in 1916. In that book the author proposed a scheme, elaborated and modified in subsequent publications, on which most of the field work on the successional relations of types of vegetation in the British Empire during the last decade or so has been based. Many phenomena of the kind described by Mr Michelmore find a place in Clements' scheme as elaborated by himself and by subsequent workers. We are far indeed from having reached finality, active criticism and revision are constantly needed, but no good purpose is served by ignoring a considerable body of related concepts already applied, tested, and some of them criticised, by numerous workers in this field.

Prof. Phillips will reply to Mr Michelmore's letter in a short article, dealing with succession, the climax, etc., to appear in our next issue.—EDITOR, *Journ. Ecol.*]

REVIEWS

Elton, Charles. *The Ecology of Animals.* Pp. 97, 6½ × 4 inches. Methuen's Monographs on Biological Subjects, edited by G. R. de Beer. London, Methuen and Co., Ltd., 36 Essex Street, W.C. 2. Price 3*s.* 6*d.* 1933.

Elton, Charles. *Exploring the Animal World.* Pp. 119, 7¼ × 4¾ inches, with 3 woodcuts by Nora S. Unwin. London, George Allen and Unwin, Ltd., 40 Museum Street, W.C. 1. Price 3*s.* 6*d.* 1933.

Mr Elton's two little books are welcome evidence of the increasing popularity and importance of Animal Ecology. The first, which is the longer, though it has the smaller number of pages, belongs to Dr de Beer's excellent three-and-sixpenny series, and is intended as an elementary introduction for those who may become serious students of the subject. The chapter headings will give some idea of its scope—"The Scope of Animal Ecology," "Ecological Surveys," "Animal Inter-relations," "Habitats," "Numbers—Statistics and Dynamics," "Economic Problems." The book is packed with items of information of interest to all ecologists. One of these is the accumulating evidence that animals sometimes choose their habitats not for reasons involving survival value, but because they like them, and that they may avoid others which they dislike but which we cannot believe are in any way dangerous or biologically disadvantageous. It is a question whether such "psychological" behaviour has any relation to natural selection. Another interesting point brought out by Mr Elton is the comparatively narrow limits of variation in the number of species of animals inhabiting any given limited habitat. The fluctuations in the numbers of individuals of a given species from year to year, and the cycles of rise and fall in the size of animal populations are topics now undergoing the most rapid current development, and in which Mr Elton himself is a leading worker and authority. The ultimate causes of the cycles are still largely obscure, but the author shows clearly that the fluctuations of different species are often causally and closely interlocked.

Exploring the Animal World is based on a series of broadcast talks, and forms a most attractive introduction to the subject for the plain man. Many of the same topics are dealt with, and the whole is leavened with the author's characteristic quiet and often whimsical humour. That the material made attractive and fruitful broadcasts is shown by the fact, mentioned in the preface, that an inquiry into woodland bird life was carried out with the help of various listeners; the results will be published in the *Journal of Animal Ecology.* Miss Unwin's three woodcuts show considerable sense of decoration and certainly embellish the book; one would indeed have welcomed three times as many, especially if they had all been closely related to the situations described by the author.

A. G. T.

Horwood, A. R. and the late **Earl of Gainsborough.** *The Flora of Leicestershire and Rutland: a topographical, ecological and historical account, with biographies of former botanists.* Pp. ccxcvii + 687, 7½ × 5 inches, 26 plates, a topographical and a geological map. Oxford University Press. Price 35*s.* net. 1933.

This lengthy book (for not only does it contain nearly 1000 pages in all but the type is small) is notable for containing a good deal more information of value to the ecologist than is to be found in most county floras. There are nearly 300 pages in the introductory part, and of those only a little over 60 are devoted to biographical matter and the history of botanical investigation, which figure so largely in many local floras. Besides the usual sections on Geology, Soils, Climate, etc., the relation of agriculture to natural vegetation is discussed (with a good deal about the famous Leicestershire pastures), the "botanical districts" are described topographically and physiographically, long lists of species are given, and there is also a section on natural types of vegetation. In this last the nomenclature and treatment follow, on the whole, the usage of *Types of British Vegetation.*

In the systematic part, besides the usual information about each species, including its distribution in the different "botanical districts," its occurrence on the various geological formations, on the different soil types and in the types of plant community recognised is usefully added.

This flora, which must have involved an enormous amount of field, herbarium and literary work, contains a large body of information and is a valuable addition to our county floras.

There is an index to the subjects dealt with in the introductory part, but none to the species described in the systematic part, an omission which makes reference difficult.

A. G. T.

THE NOVEMBER ISSUE OF *THE JOURNAL OF ANIMAL ECOLOGY* (VOL. II, NO. 2)

This number contains ten papers, two notes, ninety brief notices of British publications on animal ecology, and five reviews. David Lack, in a long and important paper, brings forward evidence that psychological preferences play a large part in determining habitat selection by birds. He bases this conclusion upon observations made on the birds living in forest plantations of different ages on Breckland. R. E. Moreau, however, gives an account of the distribution of the vulturine fish-eagle of Africa, showing that this bird is closely associated with a particular species of palm, whose nuts contain an oil rich in vitamin A. Several papers deal with ecology in various parts of the Empire. C. H. N. Jackson describes a method of estimating the absolute density of tsetse flies in a semi-isolated area of Tanganyika forest, and also gives a note on methods of marking the flies with spots of paint. T. A. M. Nash works out the correlation of tsetse with various climatic factors, by means of statistical methods. The influence of light conditions on habitat selection in two species of blowflies is recorded by F. G. Holdaway, while the nocturnal behaviour and activity of rain-forest vertebrates in British Guiana are described by C. Crawford. The diurnal rhythms in voles also receive attention in a study by D. H. S. Davis, who demonstrates the existence also of a short-period feeding-rhythm. A study by J. Eliot Moss of the parasites and other factors controlling the numbers of cabbage white caterpillars has bearings both on economic questions and on evolution theories: special place is given to a discussion of the mimicry hypothesis. Freshwater biology is represented by J. E. Duffield's study of fluctuations among crayfish in some rivers near Oxford, based on the records of a number of amateur observers, and G. V. Nikolski's survey of the fish fauna of some Central Asiatic rivers, with special reference to the relation between fish and rate of stream-flow. A note by W. B. Alexander confirms the suggestion that foreign immigrant rooks mostly haunt eastern England and therefore do not upset calculations about Oxfordshire rook roosts. Reviews deal with the August issue of the *Journal of Ecology*, zonation of marine bottom and intertidal animal communities, tropical social wasps, and methods of collecting and preserving birds and mammals.

Charles Elton.

BRITISH EMPIRE VEGETATION COMMITTEE

DISCONTINUANCE OF B.E.V. ABSTRACTS

THE British Empire Vegetation Committee have decided, with much regret, to discontinue the series of abstracts which have been appearing in the *Journal of Ecology* since 1928; and the instalment which appeared in vol. XXI, No. 2 (August, 1933) is the last which will be issued. In all 822 abstracts have been published.

When the scheme was started it was intended that authors of ecological books and papers relating to the Overseas Empire should send abstracts of their published work to the Committee, and a number of "collaborators" in this country were appointed to edit the abstracts relating to different regions of the Empire, and at the same time to keep an eye on the publication of such work, themselves supplying abstracts of papers whose authors had not responded to the scheme (see this JOURN. **15**, 376). Authors of ecological publications in the Empire have not in fact responded to the scheme at all generally, and very few authors' abstracts have been received. The result has been that nearly the whole burden of writing the abstracts has fallen on the collaborators, and they have had to carry out an unreasonably large amount of unpaid work. Under these circumstances it has proved impossible to secure even approximate completeness of record, so that the series of abstracts has lost a good deal of its potential value. The difficulty of organising a really satisfactory system of abstracts of scientific books and papers is well known, and it is with regret that the Committee have to confess to their failure to obtain the success which had been hoped for on this side of their work. Meanwhile the collaborators deserve the most cordial gratitude, not only of the Committee, but of all readers of the *Journal* who have found the series of abstracts useful, for so faithfully carrying out a task which has proved unexpectedly laborious and rather thankless. The Committee have not felt justified in asking them to continue it any longer.

With regard to the other sides of the Committee's work it is satisfactory to be able to report that more than four-fifths of the edition of 2000 copies of *Aims and Methods in the Study of Vegetation*, published in 1926, have been sold. Reports that have come to hand from time to time make it clear that the book has been of very considerable use to workers in outlying parts of the Empire. In spite of the low price at which the book was published there is a total profit of more than £400, owing to the elimination of the "middle man" in the distribution of the book. This was made possible by much voluntary work on the part of distributors in different parts of the Empire, and by the generous co-operation of the Crown Agents for the Colonies. The Committee have invested these profits in Government Stock and are holding the money with a view to its useful employment in the future, probably in the financing of one or two specimen *Handbooks* of the vegetation of regions of the Overseas Empire. Owing to the deeply lamented death in 1931 of Dr Chipp, the Secretary of the Committee, the scheme for the preparation of these handbooks received a severe setback; but the Committee have now been in communication with prospective authors and it is hoped that one or two may be ready for publication in two or three years' time.

BRITISH ECOLOGICAL SOCIETY

SUMMER MEETING AT EAST DEAN, SUSSEX, AUGUST 12TH–14TH, 1933.

THE Summer Excursion of the Society was held in the Goodwood beech forest area of the South Downs on August 12th, 13th and 14th. The village of East Dean was made the excursion centre and about twenty members attended. Dr A. S. Watt conducted the party over a route designed to illustrate the successional relationships of the beech- and yew-woods of the area. These have been fully described by Dr Watt in different numbers of the *Journal*, and the excursion afforded an excellent field demonstration of the major results of his investigations.

Saturday, August 12th. From the "Trundle," an isolated eminence (677 ft.) standing opposite the Goodwood racecourse, an excellent view was obtained over the excursion territory: to the north lay the dip slope of the main chalk ridge heavily wooded with beech, oak-hazel coppice and plantations of Conifers. Charlton and Singleton forests with post- and pre-war clearing were quite clearly visible. In contrast to the northern view, to the south lay open grassland country and to the west the yew-wood of Kingley Vale. In the immediate neighbourhood of the "Trundle" were demonstrated sub-spontaneous pinewood on chalk and phases of very rich beech woodland regeneration attributable to the full mast years of 1900, 1906, 1911 and 1922.

The party proceeded to Eartham Wood, visiting an area of beechwood felled during the War, now in an early phase of sub-seral development and dominance by ash. From the ridge just outside Eartham Wood a good view was obtained of a series of valleys (coombes) debouching south and south-east from the main chalk ridge. These were shown to exhibit successive stages in the development of wood vegetation: scrub; scrub invaded by ash; modified ashwood; beechwood. On steep exposed slopes the succession is from juniper scrub direct to beechwood: on sheltered slopes from hawthorn scrub through ashwood to beechwood. Colonisation by woody plants begins in the most sheltered part of the coombe (the north-west corner) and radiates outwards from there, the rate of spread showing a definite relation to exposure to wind. The wind effect is also seen in the relative widths of the ash-oak associes on the exposed and the sheltered sides of beechwood.

In the afternoon the party visited the magnificent yew-woods of Kingley Vale. The initial stages of colonisation by scrub were widely represented by *Crataegus* on the sheltered valley slopes and juniper on the rest. The dependence of the yew on the presence of this protective scrub was very clearly demonstrated by the presence of young yews growing out of the middle of rabbit-attacked *Juniperus* and *Crataegus* bushes. The oldest part of the wood occupied the sheltered north-western slope of the coombe, and phases of succession towards this through juniper scrub, yew scrub and young yew-wood were clearly evident. Within the older yew-wood the collapse of pioneer yews, estimated to be perhaps a thousand years old, had allowed the entrance of scrub undergrowth and ash saplings, so that the oldest wood had the appearance of degeneration to ashwood. The floor of the valley was occupied by old yew-wood, possible originating in clumps of scrub.

Sunday, August 13th. The party entered the beechwoods at North Side, seeing at once the succession from grassland to scrub of *Crataegus* and *Prunus spinosa* through a narrow belt of the ash-oak associes with intensive shading out of scrub, up to the beech associes. After the valleys have been colonised by woody growth the communities of the succession overflow in turn on to the intervening down (plateau) where the corresponding stages from adjoining valleys gradually converge. Thus the plateau is in turn occupied by grassland, scrub, ash-oakwood and finally beechwood. Within the beechwood (associes stage) the method of regeneration by reproduction circles was demonstrated and several beautiful examples were seen of a dead pioneer oak or ash surrounded by upright ash seedlings and a fringe of straggling inward-bending young beech. The later reproduction circles showed great quantities of fallen and decaying ash and beech saplings with very tall, slender, unbranched survivors. Through the development of the ash-oak associes the progressive modification of stem and crown form (*F*1, *F*2, *F*3) were pointed out as representing successive generations of trees, reflecting in their growth progressive modification in the nature of the wood canopy. In the competition between the trees ash is first eliminated, and then oak, leading up to the early phase of the beech consocies. In Deep Coombe a dense young *Taxus* society was demonstrated in the north-west (upper) end of the valley, the same relative position as the oldest part of the yew-woods of Kingley Vale.

Monday, August 14th. In East Dean Wood the outward journey showed "*Oxalis*" and "bare" stages of the development of the even-aged beech consocies of the plateau (Sere 2), and afforded opportunity for a brief view of the down on the crest of the escarpment, and for a short examination of the development of the beech associes on the escarpment itself (Sere 4) with pioneer, semi-pioneer and straight-trunk beeches. The party returned through Charlton and Singleton Forests, in the latter seeing the late phases of internal development of the beech consocies on deeper soils (Sere 1). Here the surface loam is about 20 in. deep and has a sticky clay character: the soil depth exploited by the beechwoods is as much as 4 ft., and the tree growth and development of succeeding phases of the consocies are correspondingly rapid. Within a short distance the "bare," "*Oxalis*" and "early *Rubus*" stages of the consocies were seen. The party left the plateau forests by the great felling area now extending into the heart of Singleton Forest. There are now hundreds of acres of ground with the broken relict of former beech forests, dense *Epilobium angustifolium* and sub-seral ash actively colonising the bared region.

At 4 o'clock the party reassembled in East Dean, and before leaving thanked Dr Watt for his extremely successful leadership, and expressed their gratitude to Mrs Austin, who was responsible for the satisfactory arrangement of the local accommodation.

FUNGUS FORAY AT OXSHOTT, OCTOBER 21ST, 1933.

A fungus foray was held at Oxshott on Saturday, October 21st, in conjunction with the British Mycological Society, and under the leadership of Mr J. Ramsbottom. About eighty were present, including many students from the colleges of London University.

The route taken was through the bare pinewoods above the heath. Here most of the characteristic species were seen, but none in quantity. A course was then taken towards the Black Pond over the area which was felled during the War, then through mixed plantations back to Oxshott. Several burnt patches gave *Pyronema*, *Humaria carbonigena* and the usual Agarics found in such places.

MEETING AT CAMBRIDGE, JANUARY 2ND–4TH, 1934

SOIRÉE IN THE DEPARTMENT OF BOTANY

Members of the Society and guests were entertained at a soirée in the Botany School on the evening of Tuesday, January 2nd, when approximately ninety members and visitors were present.

A number of exhibits dealing with different aspects of plant and animal ecology had been set out. Mr V. J. Chapman showed a series of graphs and tables illustrating the effect of tidal inundation on the species and communities of the salt marshes of Scolt Head Island, and also a series of specimens of algae from the same locality, consisting chiefly of the salt-marsh species of *Enteromorpha* and their various varieties. Mr C. Diver showed a series of distribution maps of several snails and Crambidae (Lepidoptera) on South Haven Peninsula, Dorset, and by maps and collections of shells demonstrated the distribution of different phenotypes in a continuous population of the polymorphic snail, *Cepaea nemoralis*. Dr W. H. Pearsall demonstrated the operation of a Bernheim photo-voltaic cell for measuring light intensity; it is sensitive to the whole range of visible light. Dr A. D. Imms and Mr Varley put out a demonstration of living and preserved specimens of *Locusta migratoria* L. in the solitary and gregarious phases, obtained experimentally in Cambridge. Mr H. Clifford showed an exhibit of fossils obtained from Fenland peats, including fossil wood, seeds and cuticles. Dr J. A. Kitching showed an exhibit of charts and photographs recording the distribution of plants and animals on intertidal rock surfaces in a sheltered loch on the west coast of Scotland. The charts showed in particular the influence of *Ascophyllum* in preventing the growth of barnacles within its reach, and also in encouraging the growth below its fronds of many species which would probably otherwise suffer from drying up at low tide. Mr G. H. Bates put out an exhibit of photographs to illustrate the theory that the distribution of *Urtica dioica* is in close relation to the deposition of loose material on the soil surface. Mr P. W. Richards showed an exhibit illustrating light germination in four British species of *Juncus*. Dr A. S. Watt showed soil monoliths and graphs of soil analyses to illustrate the chief of the very varied soils of Breckland, and in addition a series of samples showing different stages in the development of the Festuceto-Agrostidetum from bare soil. Prof. P. A. Buxton exhibited photographs of vegetation at Gadau in the north of Nigeria (12° N., 10° E.). A number of triplets of photographs showed identical spots in the forest at the end of the dry season, and at two periods shortly after the onset of the rains. Dr R. W. Butcher showed herbarium specimens and microscopic preparations of the different types of *Zostera* found on the British coasts, and photographs illustrating the ecology of rivers. Mr E. W. Jones produced a series of dried plant specimens from Studland Heath, Dorset, which showed by the growth form of their underground parts evidence for a rising ground water table. Photographs illustrating the ecology of Wicken Fen, Kingley Vale, the Rumanian Steppe and Carpathians, and Calthorpe Broad, Norfolk, were exhibited by Dr H. Godwin, who also set out graphs and maps of permanent quadrats showing that under yearly autumnal cutting the "mixed sedge" vegetation of fenland shows marked retrogression of *Cladium mariscus* and increase of *Carex panicea*.

The thanks of the Society are due to Prof. Seward and the staff of the Botany School for having made possible this extremely interesting soirée.

ANNUAL MEETING

The twentieth Annual Meeting of the Society was held in the Botany School, Cambridge, on the following morning, Wednesday, January 3rd, at 10 a.m., the President, Prof. A. E. Boycott, F.R.S., occupying the Chair. The minutes of the previous meeting were read and confirmed. The Hon. Treasurer presented the accounts and balance-sheet of the Society, which were adopted subject to audit. It was proposed by Dr W. H. Pearsall and carried *nem. con.* that Messrs William Norman and Son, Chartered Accountants, be reappointed auditors to the Society. A sincere vote of thanks to Dr Boyd Watt for his care and skill in handling the finances of the Society was proposed by Mr C. Oldham and carried unanimously. The report of the Hon. Secretary was then read and adopted.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR YEAR ENDING 31ST DECEMBER, 1933

Income

	£	s.	d.	£	s.	d.
Subscriptions received, including arrears	281	19	7			
***less* prepayments for 1934–5**	7	7	6	274	12	1
Interest: On Investments	34	10	0			
On Deposit Account	1	0	1	35	10	1
Income Tax refunded (for 1932–3)				2	10	0
Journal of Ecology—Sales, etc.:						
Current volume XXI, 1933	440	2	0			
Back volumes and parts	45	6	3	485	8	3
Index Volume, *Journal of Ecology* (vols. I–XX)				67	6	8
Journal of Animal Ecology, vol. 2, 1933:						
Part 1: Subscriptions received	136	0	0			
Grant from Royal Society, in 1932	100	0	0			
Grant from Crown Agents for Colonies	15	0	0			
Sales	162	14	3			
	413	14	3			
Part 2: Sales, Estimated at	120	0	0			
Parts 1 and 2: Sale of Reprints	19	0	0	552	14	3
				£1418	1	4

Expenditure

	£	s.	d.	£	s.	d.
Working Expenses:						
Printing Circulars, etc.	6	19	0			
Postages, etc.	9	3	7			
Bank Charges		4	6			
Clerical Assistance (Secretary and Treasurer)	15	0	0	31	7	1
Audit Fee				3	3	0
Freshwater Biological Association of the British Empire—Grant in aid				10	0	0
Soirée Expenses				8	4	7
Library Account, Slides, etc.				18	2	3
Journal of Ecology, vol. XXI.						
Paper, Printing, Illustration, etc.	657	8	2			
Binding	4	16	3			
Postage, etc.	41	5	6			
Publishers' Commission	79	18	6	783	8	5
Index Volume, *Journal of Ecology*, (Vols. I–XX):						
Printing, Paper, etc.	148	18	9			
Expenses	5	19	3	154	18	0
Journal of Animal Ecology, vol. 2:						
Part 1: Paper, Printing, Illustration, etc.	178	18	11			
Publishers' Commission	29	5	5			
Carriage, Insurance, Advertising, etc.	16	1	5			
	224	5	9			
Part 2: Paper, Printing, etc., Account due	143	13	6	367	19	3
				1377	2	7
Balance—Surplus for the Year				40	18	9
				£1418	1	4

BALANCE SHEET AT 31ST DECEMBER, 1933

Liabilities

	£	s.	d.	£	s.	d.
Membership subscriptions, prepaid for 1934–5				7	7	6
***Journal of Animal Ecology*, vol. 2, part 2:**						
Printing Account, due	143	13	6			
***less* Sale of Reprints**	19	0	0	124	13	6
Grant from Royal Society, 1933, carried forward				50	0	0
General Revenue Account—Balance of Funds:						
Balance at 31st December, 1932	990	0	8			
***Add* Surplus at 31st December, 1933**	40	18	9	1030	19	5
				£1213	0	5

Audited and found correct and as shown by the Account Books of the Society. The Bank Balances have been verified by Bank Certificates.

(signed) WM. NORMAN & SONS,
Chartered Accountants.

120, Bishopsgate, London, E.C. 2.
12th January, 1934.

Assets

	£	s.	d.	£	s.	d.
Westminster Bank—Credit Balances:						
Current Account	77	7	5			
Deposit Account	100	0	0	177	7	5
Journal of Animal Ecology, vol. 2, part 2:						
Publishers' Account for Sales, Estimated at				120	0	0
Investments.						
£700 3½ % War Loan at cost	717	3	0			
(Market value at 31st December, 1933, at 101, £707. 0*s.* 0*d.*)						
£200 5 % Conversion Loan at cost	198	10	0			
(Market value at 31st December, 1933, at 116, £232. 0*s.* 0*d.*)				915	13	0
				£1213	0	5

Note. A further Asset is the unsold stock of the *Journals* and Index Volumes held for the Society by the Publishers.

(signed) HUGH BOYD WATT,
Hon. Treasurer.

HON. SECRETARY'S REPORT FOR THE YEAR 1933.

The Nineteenth Annual Meeting of the Society was held in the Botanical Department of University College, London, on January 7th, 1933. On the previous evening members and guests were entertained at a soirée in the Botanical Department. A large number of interesting exhibits had been arranged, and the sincere thanks of the Society are due to Prof. Salisbury for his generous hospitality.

The Summer Meeting of the Society was held in the Goodwood beech forest area on the South Downs on August 12th, 13th and 14th, from the centre of the village of East Dean. Two whole-day and one half-day excursions were made, during the course of which the beechwoods of the area were fully demonstrated in respect of their seral and developmental relations. Although the escarpment woods were also visited, attention was chiefly centred on the different seres of the dip slope, and of the coombes cutting into it. One half day was spent in exploring the magnificent yew-woods of Kingley Vale, where the full valley side sere from bush colonisation to retrogressive yew-wood was clearly demonstrated. The sincere thanks of the Society are due to Dr A. S. Watt for his kindness and competence in making arrangements for the meeting, and in demonstrating the ecological features on all the excursions.

A Fungus Foray was held at Oxshott on Saturday, October 21st, in conjunction with the British Mycological Society, and under the leadership of Mr J. Ramsbottom. About eighty were present including many students from the Colleges of London University.

Since the last Annual Meeting two further numbers of the new *Journal of Animal Ecology* have been produced, appearing in May and November, and containing respectively 128 and 178 pages. The volume includes eighteen original papers, besides notes, notices and reviews. Although this volume shows considerable increase in size over the first volume it is practically self-supporting financially at this size. There has been an increase of members of the Society taking the *Journal of Animal Ecology*: direct sales by the publishers to non-members amount to about ninety, and the Society is indebted to the Royal Society for a further grant of £50 towards the cost of production of the next volume.

During the past year two numbers of the *Journal of Ecology* have been issued containing 487 pages, supplements of 25 pages, and 22 plates. As a result of the devoted work of the Editor and his Secretary, Miss J. Salzman, a general Index to the first twenty volumes of the *Journal* has been prepared and published. The entries include the names of authors of original contributions, the names of authors of books and papers which have been reviewed or noticed, the titles of books and original and reviewed papers, the names of a large number of plant and animal species about which specific information has been given, and very full citations of topics of ecological importance. The index should greatly enhance the value of past numbers of the *Journal*.

The Society's transplant experiments at Potterne are progressing satisfactorily in the hands of Mr Marsden-Jones and Dr Turrill.

The Society has accepted Dr R. W. Butcher's generous gift of a collection of photographic prints illustrating the ecology of rivers: these will be added to the collection of the Society.

Since the end of last year the membership has risen from 305 to 322: there are 35 new members, and 18 members have resigned or died. Of the present membership list 191 members, receive the *Journal of Ecology* alone, 80 the *Journal of Animal Ecology* alone, and 50 are receiving both journals.

H. GODWIN.

The meeting proceeded to the election of officers as follows:

President: PROF. J. R. MATTHEWS.
Vice-President: MR C. OLDHAM.
Council Members: PROF. A. E. BOYCOTT, F.R.S., DR E. S. RUSSELL.
Hon. Editor of the Journal of Ecology: PROF. A. G. TANSLEY, F.R.S.
Hon. Editor of the Journal of Animal Ecology: MR C. S. ELTON.
Hon. Secretary: DR H. GODWIN.

In recognition of the extreme value of their pioneer work in ecology both to the subject as a whole and to this Society in particular, Prof. H. C. Cowles and Dr L. Cockayne, F.R.S., were unanimously elected to Honorary Life-Membership.

Dr W. B. Turrill gave an account of the progress of the transplant experiments of the Society at Potterne. They have now been successfully administered for six years by Mr E. Marsden-Jones and Dr Turrill, and a third report is now in preparation for publication. A grant of £5 towards the cost of the experiments in 1934 was proposed and carried.

Mr P. W. Richards then gave an account of the tropical forest vegetation in the region of Mount Dulit, Sarawak. He distinguished three types of climax forest: (1) The *Lowland Mixed forest*, on clay soils below about 1000 m., with little tendency towards dominance by individual species and with prevalent buttressing of the trees. (2) The *Lowland Heath forest*, an edaphic type of lowland rain-forest limited to sandy soils and characterised by a strong tendency towards dominance of a single species, by its openness and by the relative absence of buttressing. (3) The *Montane forest*, or *Moss forest*, growing on water-logged soils above 1000 or 1100 m., with small sclerophyll trees very densely covered with epiphytic bryophyta and with a flora extremely divergent from that of the lowland forests, especially in its large content of species belonging to the Australian floral element. Mr Richards pointed out that moss forest had been previously described from other tropical regions, and showed that the Mixed Lowland and Lowland Heath forest types of Borneo were comparable in almost all respects, save systematic position of the component species, with the Mixed Lowland and Wallaba forests he had previously described from British Guiana.

Dr W. H. Pearsall then gave an account of the use of the Bernheim photo-voltaic cell in measuring the penetration of light of different wave-lengths into the waters of Lake Windermere, Ennerdale and Esthwaite Water. The quality of the light at the lower limit of phanerogamic vegetation is very dissimilar in these different lakes. The lower limit of vegetation shows no good correlation with the total quantity of light penetrating to this depth, but figures were given suggesting good correlation with the penetration of red light. Curves were produced to show seasonal and yearly variations in light penetration in these lakes, and it was pointed out that recent increase in sewage inflow, by increasing the phytoplankton and so diminishing light penetration, had caused shallowing of the lower limit of growth of aquatic phanerogams.

Mr G. H. Bates put forward the results of an extremely interesting survey of the distribution of a large number of nettle (*Urtica dioica*) populations. He pointed out that in the great majority of cases they occurred with surface litter, such as with stone, sand or gravel heaps, under hedge clippings, in hedgerows, under heaps of mown grass, and at the foot of walls of farm buildings. He suggested that in these cases it was the loose character of the surface soil and protection from light which determined the presence of nettles, rather than the nitrogen factor which is generally assumed to be responsible. Nettles were even found associated with heaps of drain pipes and of scrap iron. Such facts and preliminary nitrogen estimations led Mr Bates to the conclusion that high nitrogen supply is seldom an important controlling factor, despite Olsen's results. This conclusion was both supported and criticised in the ensuing discussion.

Mr P. Falk then gave a description of the vegetation of the lava desert of central Iceland. The lava weathers so rapidly and forms such a porous soil that it is almost totally devoid of vegetation, save very scattered plants of *Armeria maritima*, *Silene maritima* and *Arabis petraea*. In this desert there are oases of three types: (1) local depressions of non-porous rock associated with springs or rivers: these show a vegetational zonation determined by the height of soil above the water-table, with an outer fringe of dunes on the desert edge, covered with *Elymus arenarius*; (2) areas round hot springs: here not only increased temperature and higher humidity are important ecologically, but the deposition of calcium carbonate from solution serves as a binding material upon the loose rock of the valley screes, checking the extreme mobility which is a major deterrent to plant establishment; (3) mountain areas, above the scree line where the factor of soil mobility is relatively inoperative.

After the adjournment for lunch Mr C. Diver read a paper on the co-ordination of plant and animal ecology in relation to the survey of the South Haven peninsula (Dorset). He demonstrated by a series of old maps the geological history of the area since about 1600 A.D., with the recent stoppage of drainage to the sea and the extension of freshwater marshes and pools. The detailed distribution of a large number of animal species within the area had been mapped, and it was clear from such maps that they offered the most suggestive clues as to the factors controlling biotic distribution, and particularly so where correlations were evident between the distributions of specific plant and specific animal communities or individual species. Mr Diver stressed the necessity for co-operation of a large number of experts in such survey work and invited general assistance.

Dr A. S. Watt proceeded to demonstrate very effectively that soils, equally with rabbits, play an extremely important part in determining vegetational distribution in Breckland. He distinguished four chief classes of soils: (1) Sandy soils derived by leaching *in situ* from the underlying Lower Chalky Boulder Clay, and carrying very distinctive types of vegetation according to the depth of derived soil above the parent rock. The shallowest type was partly open vegetation with a number of calcicolous species; in deeper soil there were more species and complete ground cover, though still many calcicoles; in the deepest soils podsolisation had advanced considerably, the total number of species had diminished again, and included calcifuges. (2) Eroded soils resulting from truncation of podsolised soils of type (1) down to the A, B or C horizon. (3) Wind-transported soils formed during the erosion processes responsible for soils of type (2); these also are composed of material from the different podsol horizons, differing locally from one another in this respect and in vegetational cover. (4) Transitional "fen-breck" soils. Soil and vegetational analyses strongly supported Dr Watt's thesis that the vegetation is very closely related to the soil type.

Dr J. A. Kitching gave an account of investigations on the distribution of plant and animal species in the lower intertidal and sublittoral belts of the Devon and west Scottish coasts. The lowest belts had been investigated by means of a special type of diving apparatus invented for the purpose. Numerous examples were given of biotic zonation, such as that of *Laminaria digitata*, *L. Cloustoni* and *L. saccharina* at increasing depths below the spring tide low-water mark. It was shown by re-measuring denuded areas that *Balanus crenata* is a pioneer form displaced by tunicates and laminarians. By examination of sites subject to varying intensities of wave action it was demonstrated that it is possible to distinguish to some extent the relative effects upon vertical shore zonation of the diminishing light intensity and of the lessened wave action both of which accompany increasing depth.

Dr R. W. Butcher gave an account of the species of *Zostera* found on the British coasts in relation to the recently reported epidemic attacking *Zostera marina*. In addition to *Zostera marina* and *Z. nana*, there is an abundant population referred to as *Z. marina* var. *angustifolia*, and this might conceivably be a hybrid between *Z. marina* and *Z. nana*. Dr Butcher instanced numerous cases of local dying out of *Zostera* in the past and reviewed the present position with regard to determination of the causes responsible for disappearance of the plant.

The meeting closed with a hearty vote of thanks to Prof. Seward and the staff of the Cambridge Botany School for their hospitality and care in arranging the meeting, and to the lanternist for his skilled co-operation.

EXCURSION TO BRECKLAND, THURSDAY, JANUARY 4TH

On Thursday morning an excursion was made to the Breck country beyond Barton Mills. Dr A. S. Watt demonstrated in various cuttings and blow-outs the derivation of sandy Breckland soils by direct weathering *in situ* of Lower Chalky Boulder Clay. Soils of this type (1, see the account above) of different depths were shown to underlie specific types of vegetation as described in the paper given on the previous day.

The long lines of the blow-out which caused the burial of Santon Downham were shown, the floor cut down to different levels of the former podsol profile, and the sides flanked by the dunes derived from the blow-out and now covered with *Carex arenaria*, *Pteridium* or *Calluna*. The floor of the blow-out showed phases of colonisation of bare sand by *Polytrichum*, and transition through lichen communities to grass-heath, or *via* surface erosion to bare ground again.

LIST OF MEMBERS (JANUARY 23rd, 1934)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, DR H. GODWIN, Botany School, Cambridge.

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ERRATUM

Vol. XXI, p. 350 and Vol. XXII, p. 106.

T. A. W. Davis, one of the authors of the paper on "The Vegetation of Moraballi Creek," should be described as "Dip. For. (Oxon.)," not "B.A."

VOLUME XXII AUGUST, 1934 No. 2

THE VEGETATION OF AKPATOK ISLAND. PART

BY NICHOLAS POLUNIN.

(*Christ Church, Oxford; Henry Fellow at Yale University.*)

(*With Plates* XXVII–XXXIX *and three Figures in the Text.*)

CONTENTS.

PAGE
INTRODUCTION 338
- Climate 343
- Comparison with other regions 344
- Flora 345
- Recognition of habitats 346
- Methods of work 346
- Acknowledgments 347

HABITATS AND SPECIAL COMMUNITIES 348
- I. Hill-tops 350
  - (*a*) Barren limestone splinters 350
  - (*b*) Fjaeldmark including larger limestone blocks 350
  - (*c*) Polygons 351
- II. Plateau 352
  - (*a*) Stone polygons 352
  - (*b*) Non-polygon "fjaeldmark" etc. 363
  - (*c*) Peculiar areas 366
- III. Screes and other slopes 367
  - (*a*) Partially stabilised screes 367
  - (*b*) Barren unstable screes of jagged particles 370
  - (*c*) Rough but stabilised "old" dry slopes 371
  - (*d*) Damper, less steep *Oxyria* slope 372
  - (*e*) Slopes with wet earthy tracts 373
  - (*f*) Sandy *Dryas* slopes 373
  - (*g*) Dry earthy screes 375
- IV. Ravines 376
- V. Valley sides 377
  - (*a*) Damper, better vegetated valley slopes 377
  - (*b*) Poorer, dry valley slopes 379
  - (*c*) Grassy valley sides 380
- VI. Valley heads and depressions 381
  - (*a*) Lake marginal zonation 381
  - (*b*) Boggy dips without lake 382
- VII. Snow effect 383
  - (*a*) Swallow holes 383
  - (*b*) Late snow patches 385
  - (*c*) Persistent snow patches 389
- VIII. Erratic boulders 391
  - (*a*) Exposed on plateau 391
  - (*b*) Sheltered 392
  - (*c*) Of stream bed 393

REFERENCES 395

INTRODUCTION.

The adventures of the Oxford University Expedition to Akpatok Island have already been described in a lecture (**1**), and more fully in a book (**2**) which gives some account of the extraordinary climatic and other conditions, as well as an interspersed commentary on the flora and fauna and on the main geological features. A party of ten graduates and undergraduates, including a zoologist, a geologist and myself as botanist, we chartered a sealing schooner in the summer of 1931 at St John's, and with a crew of six stalwart Newfoundlanders sailed up the Labrador coast, putting in for shelter at many points. Then, and on the return voyage, I was able to make collections and the roughest of ecological surveys at points never more than 250 miles apart along this stretch of 1100 miles of North Atlantic seaboard. At Akpatok a more detailed survey was carried out, and the botanical specimens having now been identified it becomes possible to present a systematic account of my observations.

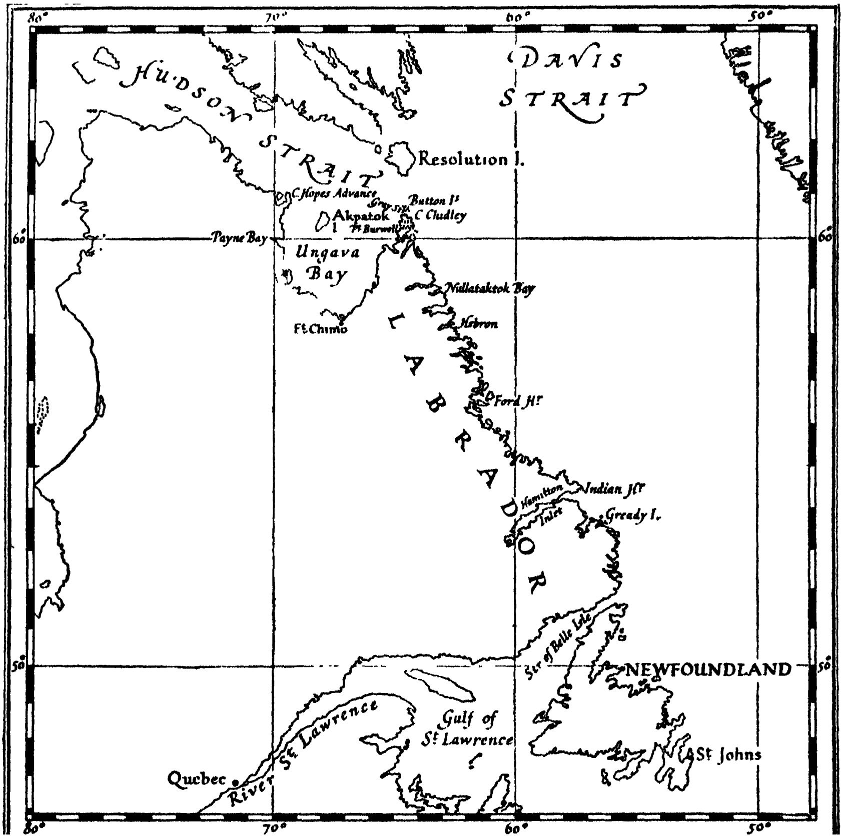

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Fig. 1.

Akpatok Island lies at about latitude 60° 25′ N. and longitude 68° W. in the mouth of Ungava Bay, to the south of Hudson Strait (see Fig. 1). The charts marked it vaguely as a large island with rugged uneven coasts and a varying number of lesser isles, we found it, as the present map shows (Fig 2), no more

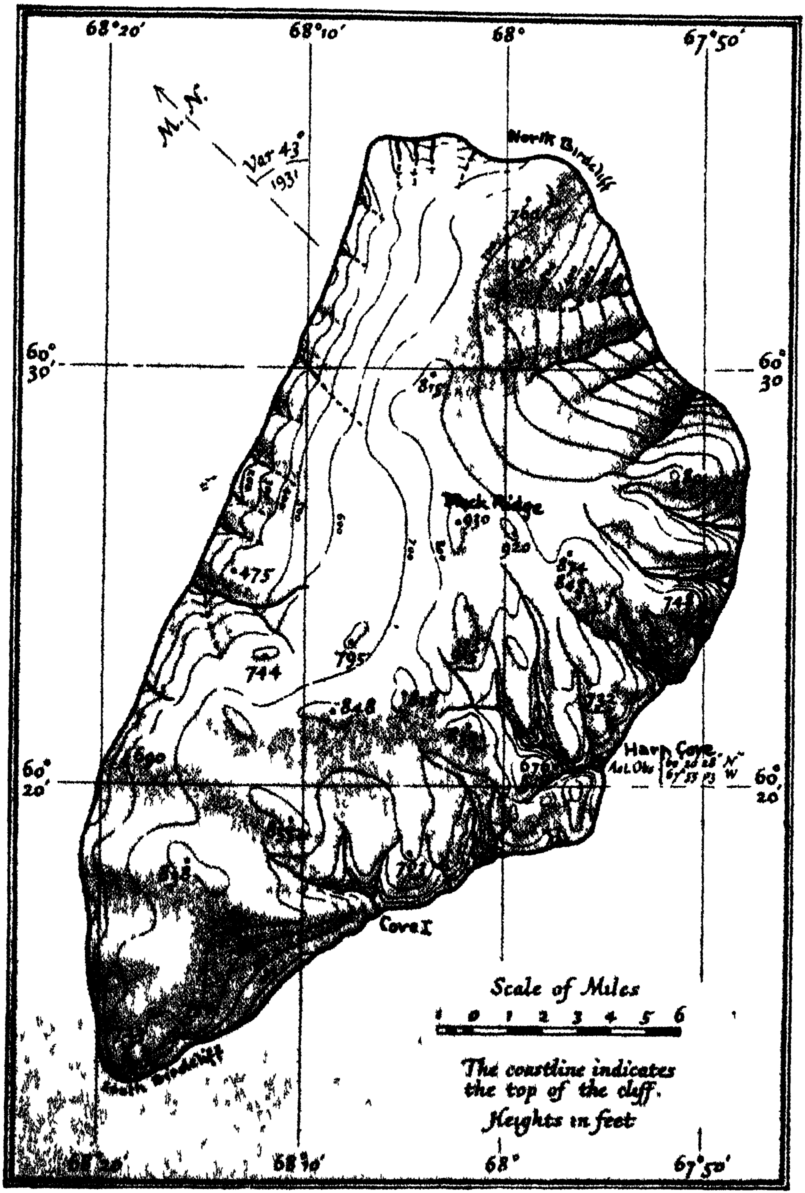

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FIG 2 Akpatok Island.

than 30 miles long and with a singularly regular coastline unaccompanied by the smallest islet! Unvisited save by occasional parties of seal and walrushunting Eskimo, and inhabited only by polar bears, Arctic foxes and birds, its physiographic features were at once unforgettably striking, as was the extreme poverty of the vegetation over most of its area.

The island is formed entirely of horizontally bedded Ordovician limestone, which almost everywhere on the coast forms great perpendicular cliffs rising from 300 to over 600 ft. sheer out of the water at high tide. The coastline is unbroken by any large indentations, so that these light-coloured limestone cliffs, with their exact horizontal stratification and level tops of even height running continuously straight for many miles, are most impressive (see Pl. XXVII, phots. 1 and 2, though more often there is no scree). Except where it is colonised by nesting sea-birds the cliff face itself is almost always quite barren, as is the small bank of shingle which generally collects at its base, in the angle formed with the marine shelf (see Pl. XXVII, phots. 1 and 3) which in most places extends a hundred yards or more seawards. This shelf is uncovered only at low tide, when the photos were taken, and is also largely barren, being so scoured by heavy seas and the grinding action of ice in winter that the few small algae existing in its more sheltered pools are probably all annuals. Nor are any larger algae visible below low-tide mark, but farther out at greater depths grow enormously long Laminarians.

The tops of the cliffs are also light in colour (see Pl. XXVIII, phot. 4, and phot. 5 of low weather-beaten cliffs on the west coast), being largely shorn of vegetation by the wind. Inland extends a monotonous, gently undulating plateau (see Pl. XXIX, phot. 6) which constitutes almost the whole of the 300 odd square miles of the island. When the sky is overcast this plateau is of a dull grey, having its limestone surface frost-shattered and otherwise weathered into irregular particles of all sizes. The smaller particles form a fine silt, which becomes arranged in definite polygonal or rounded areas delimited by intervening tracts (see Fig. 3) composed of the larger stones, which may be of almost any size. Most of the surface of the plateau (i.e. of the whole island) is of this nature, and supports only a sparse open community of dwarfed herbs and ground shrubs.

The polygons are generally 2½–5 ft. (0·75–1·5 m.) in diameter, of compact soil which often remains damp and clayey (see Pl. XXX, phots. 10 and 11). They seem to be dynamic and rarely support any plants at all, in contrast with the slightly raised network of narrow intervening tracts (6 ins. to 1 ft. across) which are well drained and aerated, and support close dark tussocks of *Dryas integrifolia*[1] and flat-pressed bushlets of *Salix arctica*. These latter may extend a foot or more laterally but never rise more than 2 or 3 in. (5 or 7·5 cm.) above the surface, even when their thick-barked axes show as many as twenty-five annual rings. There are no trees or even examples of *Betula nana* on the island, the tallest plants being occasional shoots of *Carex misandra* and grasses. In favourable localities, these may reach a foot in height, but not on

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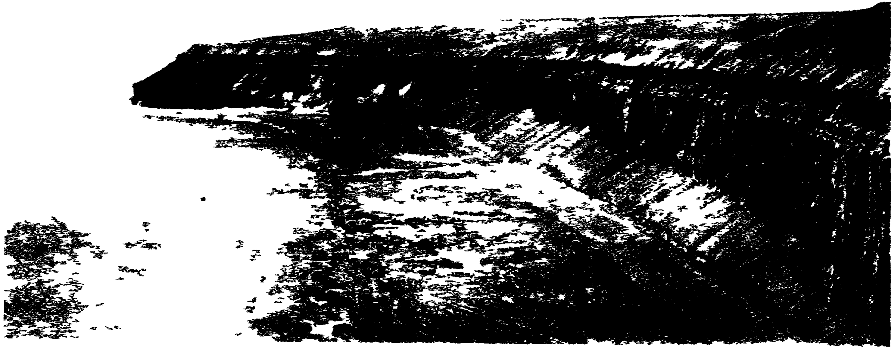
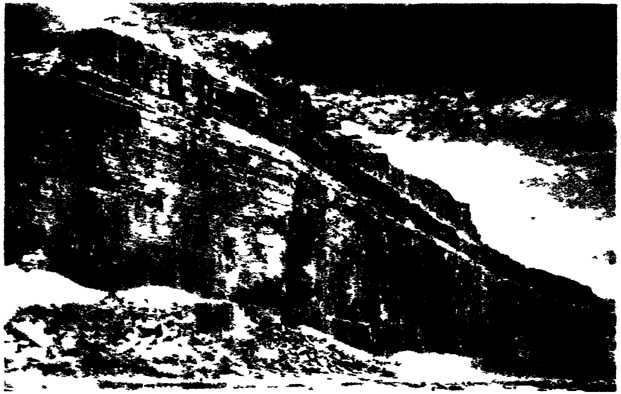
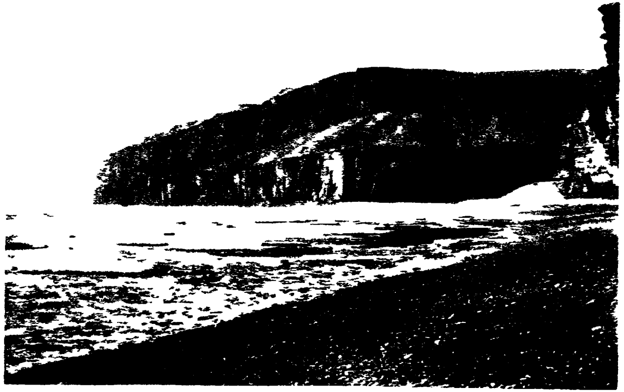
[1] The authorities for the names of all plants occurring on the island will be found in "The flora of Akpatok" (**20**).



Phot 1 Akpatok cliffs showing characteristic horizontal strata, screes (200 ft long and limestone shelf which will be covered at high tide (p 340)



Phot 2 Akpatok cliffs, always of limestone and here about 600 ft high (p 340) Rough talus slopes below (p 371)



Phot 3 Entrance to a broad ravine Harp Cove shore at low tide showing shingle bank and limestone shelf (p 340)

the plateau itself. Other associated plants are *Saxifraga oppositifolia* and *S. aizoides* (generally both fairly frequent), with Drabae and small mosses, and lichens including conspicuous white patches of *Cetraria nivalis* and brown patches of *C. islandica*.

Dryas is the chief angiosperm dominant, generally forming at least the central tussock of these streaks of vegetation on the borders of the polygons (see Pl. XXX, phot. 10). Sometimes the whole of an intervening tract between two polygons is closely covered (as in places in Pl. XXX, phot. 10), but as often as not it is largely barren, even in an area which appears relatively favourable. On a rough estimate an ordinary plateau region might have about one-eighth of its area covered by vegetation in the form of streaks or irregular patches or more sparsely scattered plants; such polygon-covered areas may stretch for miles and miles. Since the facies of better developed vegetation (and occasional localised areas with closed vegetation) are more than compensated for by larger areas with hardly any plants at all, it is probable that the surface of the island as a whole is less than one-eighth occupied by plants. Thus the plateau has the appearance of a great grey desert strewn with jagged splinters or blocks of limestone and dotted here thickly and there sparsely with small dark patches of vegetation, the bare space between glaring white or yellow under the intense illumination of the summer sun (see Pl. XXIX, phot. 6).

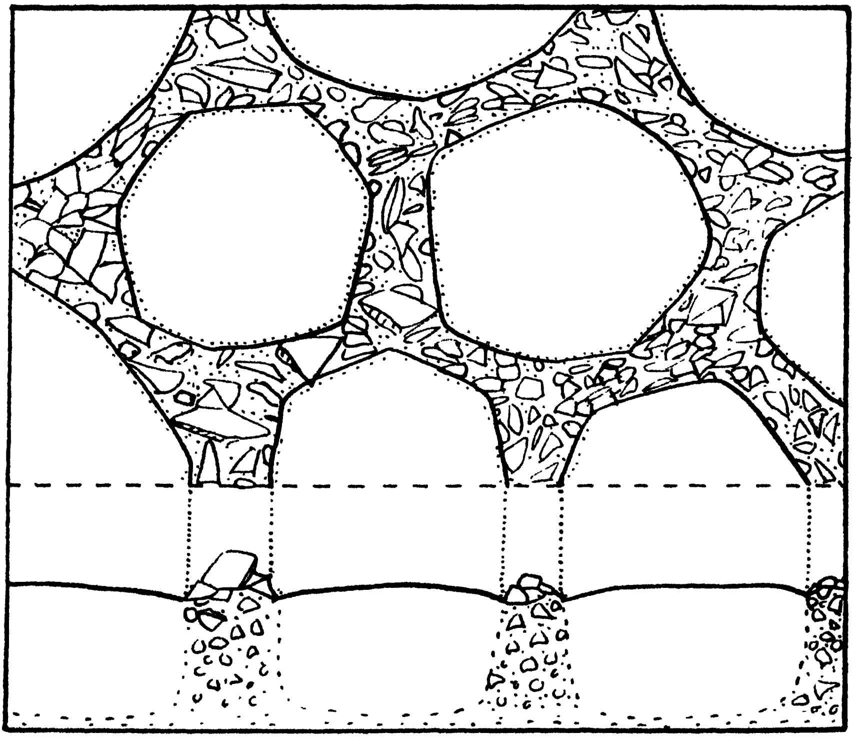


FIG. 3. Stone polygons and intervening tracts: surface and sectional views.

Even less vegetated than these plateau barrens are the frequent hills. In a few cases they rise to a total altitude of over 900 ft. (although not more than some 300 ft. above the average level of the plateau), but even the highest hills are rarely distinctive, having rounded tops scarcely making features of contrast with the surrounding plateau. Few higher plants occur, for drainage is good and frost comminution consequently less active; little soil is made, the surface being littered with blocks or splinters of limestone which on the most exposed hill-tops hardly support even a speck of crustaceous lichen.

The main relief to this rolling country is afforded by watercourses (see Pl. XXIX, phot. 7), although these were for the most part dry by the middle of August when we arrived on the island. They start near an ill-defined watershed or a patch of melting snow (Pl. XXIX, phot. 8) as shallow depressions with gently sloping sides, but towards the sea they deepen, with steeper sides, till finally they become ravines, in many cases so deep on the coast that they have cut right down through the cliffs to the sea-level[1]. Thus much of the interior plateau is dissected by dry ditches, while the ravines near the coast have their sides formed by cliffs or by dynamic screes (Pl. XXXII, phot. 15), and rocky beds covered by running water when the snow melts—the whole very often entirely devoid of plants.

In some ravines small streams of water persist throughout the summer, while other streams cascade over the tops of the cliffs or gush from lips partway down their faces. These streams are fed most often from open water which in the form of numerous small lakes is abundant in places on the plateau, sometimes almost filling the slightest of depressions. The lakes are generally very shallow (Pl. XXXVI, phot. 30) and either persist with little change in level or lose their water quickly and suddenly, the probable key to permanence being a continuously frozen subsoil, for some areas are drained not by exposed watercourses but by swallow holes in the porous limestone.

The margins and beds of temporary lakes are generally as barren as those of the watercourses. But in marked contrast with what was at best a sparse open vegetation in all the habitats described above, we have the damp sheltered depressions and occasional more extensive valleys where conditions are so much better that the vegetation may be closed and quite luxuriant, giving a dark colour to the area. The depression may be slight in a light-coloured region of limestone plateau, but if snow can collect in winter the whole aspect will be changed (see Pl. XXXIX, phot. 37). *Salix arctica, Carex membranopacta* and grasses are the chief plants of such situations, often forming a closed community with or without mosses of tufted growth. In damper areas little peaty hillocks may be formed, while the wettest bogs, especially (around the margins of some of the more permanent lakes, support fine beds of *Eriophorum* and *Arctagrostis latifolia* (Pl. XXXVI, phot. 30).

Better drained, dry areas which in winter are protected by a kindly blanket

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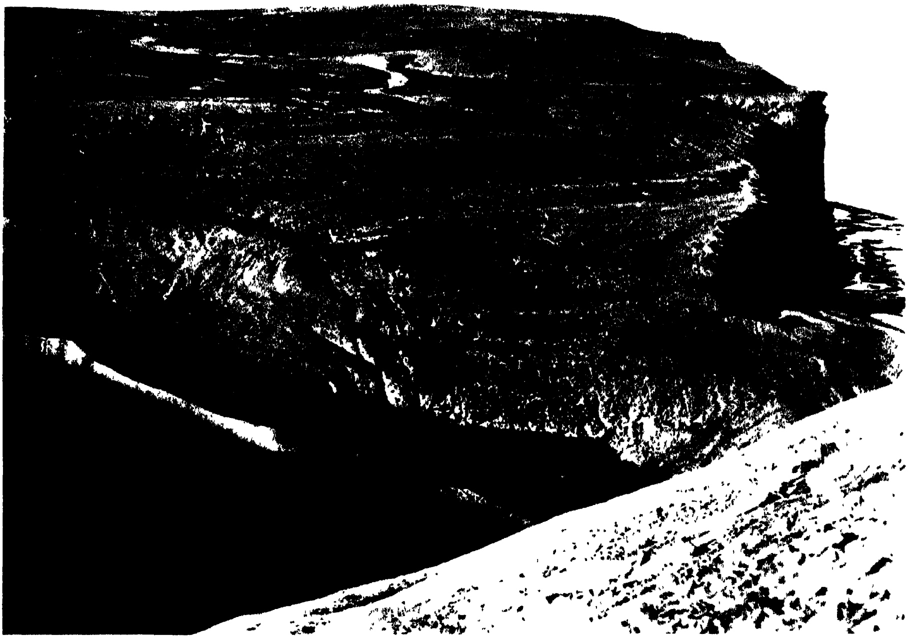
[1] This sequence is illustrated by Pls. XXXIV and XXXV, phots. 24–27, which show typical ravines of various ages.



Phot. 4. The plateau of Akpatok Island near the coast, showing characteristic cliffs from above, and expedition tents in valley bottom (p. 340).

Phot. 5. Low cliffs on the west coast of the island, with light-coloured, rounded tops all much weathered, and quite barren (p. 363).

of snow, may be vegetated by a close heat-mat of ground-shrubs about 4 in. high[1], chiefly dominated by *Cassiope tetragona* but including *Empetrum*, *Rhododendron lapponicum* and *Vaccinium uliginosum* var. *microphyllum*. Where the snow drifts behind ridges and persists well into the growing season there is developed a dwarf "late snow" community of almost pure *Salix herbacea*, recognised from a distance by its exceptionally dark colour, while areas where the snow melts still later in the summer, and which remain wet for a long time, support only a mixed open community of *Oxyria digyna* and *Saxifraga* spp.

There is much evidence of glaciation of the island—large erratic boulders (see Pl. XXXIX, phot. 37) of mica schist, strewn about some parts of the plateau and looking like resting herds of black cattle, occasional conical deposits a few feet high of quartz sand left by receding glaciers, and one or two more extensive moraines of mixed sand and boulders. These "acidic" deposits, restricted to the higher parts of the island, form almost the only distinctive landmarks, and are recognised by their irregular outline and dark colour. This is intensified by the more luxuriant if peculiar vegetation they support, as is exemplified by the "Black Ridge" which stands up in the middle of the island. Other still more exceptional and localised habitats are afforded by the "bird-cliffs" at the north and south ends, above which a thick lush patchwork quilt of mixed and many coloured mosses and lichens is developed.

All the habitats and communities that were noted are listed on pp. 348 and 349, whence reference can be made to the sections in which they are considered more fully.

CLIMATE.

The edaphic and geodynamic factors obtaining almost everywhere on Akpatok are extremely adverse to plant growth, the universal limestone substratum aggravating problems of instability, local drought due to porosity, non-accumulation of humus, and lack of combined nitrogen. Moreover, the direct effect of the climatic factors is so severe as to cause the habitats produced to be unfavourable to a degree that makes extreme poverty the most striking feature of the vegetation, which is of a high Arctic type in spite of the comparative lowness of the latitude. The biotic factor is on the other hand probably of little importance, but the soil water is almost everywhere neutral or alkaline, and never very acid.

Statistics furnished by the meteorologist of the expedition give the mean day temperature at the end of August as 48° F. and the night temperature a bare 1° lower, with humidities of 70 and 80 per cent. respectively. In September the humidity increased to 90 per cent. at night which made the air feel cold although the temperature did not fall below freezing-point until the middle of the month. All this goes to suggest that conditions are relatively favourable in summer though the growing season is of course very short; but it must be remembered that 1931 was an exceptionally good year, vague reports giving the region as almost continually fogbound or gale-blasted in ordinary times; indeed it is "one of the few places where you can get fog and a gale at one and the same time[1]," and that is apparently frequent. Thus, in spite of its geographical position and the prevalence of the north-westerly winds common to the greater part of north Canada and Labrador, Akpatok has an oceanic climate, at least in summer. The shore ice moves off between June 20th and July 20th[2], while the temperature of the sea water near the coast from August 20th to September 20th was between 36 and 38° F. in 1931.

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[1] These late snow communities are illustrated in the sequence of Pls. XXXVII and XXXVIII, phots. 31–35. The ameliorating effect of a thick covering of snow is discussed in (**22**) and (**23**).

The reasons for the extreme poverty of the land vegetation are, first and foremost, the exposed nature of the predominating plateau—generally quite unprotected from the rigours of the proverbial gales of the district, which sweep it bare of any protective snow covering in winter and, added to the basic effect of a hard and truly Arctic climate, make conditions extremely difficult for plant growth. The snowfall is probably small and combined nitrogen almost everywhere seriously deficient, while in summer rain and frequent fogs cut down the light and heat-giving radiant energy supply of an already short growing season. At other times a desiccating gale will be blowing, and finally, with its alkalinity and lack of food substances, and its porosity causing local surface aridity and drought, we have the everlasting limestone!

COMPARISON WITH OTHER REGIONS.

Altogether it is not at all surprising to find the vegetation of the plateau, and indeed of the whole island, comparing most unfavourably with that of the adjacent mainland. There most of the habitats are more sheltered and support closed communities (cf. Pl. XXXI, phot. 12 of Port Burwell), and the rocks being acidic and non-porous allow humus to accumulate. When we come to more general comparisons with other northern regions, both the flora and fauna, and particularly the luxuriance of their development, seem especially poor for an island of continental position, no matter what the latitude. Collections made by the Oxford West Greenland Expedition in 1928 show that the flora and fauna of Godthaab Fjord are considerably richer than those of Akpatok, though Godthaab Fjord is some 300 miles farther north. Again, many parts of Baffin Land are much better vegetated, especially the sheltered valleys, and so is the Atlantic coast of Labrador at the same latitude as Akpatok; on the eastern coast of North America we have to go north to Ellesmere Land at a latitude of nearly 80° N. to find such barrenness as Akpatok Island shows.

Farther afield we may consider north Norwegian Lapland at latitude 70° N.; with birch forest extending to an altitude of over 1000 ft., the flora and vegetation are incomparably richer, as are those of the Kola Peninsula and the shores of the White Sea. So are even the most exposed islands of the Arctic coast of Scandinavia, and also Kolguev in Barents Sea where the influence of the Gulf Stream is no longer felt. On Bear Island, which at latitude 74° 30′ N. is oceanic in both position and climate, and again in places on Spitsbergen at nearly 80° N., we at last find flora, fauna and vegetation as poor as on typical areas of Akpatok only just above the sixtieth parallel, while again on this side of the Atlantic we have to go to Franz Josef Land, lying around latitude 81° N., to find them definitely much poorer.

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[1] The President of the Royal Geographical Society, Admiral Sir William Goodenough, in a discussion on the work of the expedition.

[2] *Sailing directions for the Hudson Bay Route*, Ottawa, Dept. of Marine, 1932.

FLORA.

In spite of all that has been said about the poverty of the vegetation and the adverse conditions under which the plants eke out their precarious existence, the aggregate flora of Akpatok is perhaps considerable, having regard to the comparatively small size and isolation of the island, its completely exposed surface and its specialised limestone "soil." Certainly in view of the very few species to be met with in an ordinary walk over the plateau which constitutes almost the whole area, the lists given in the *Journal of Botany* (**20**), are surprisingly long, and depend for their dimensions largely on peculiar conditions seldom realised. Thus the bird-cliffs at the north and south ends of the island add several new species to each of the main phyla, and the morainic deposits of acidic rocks bring in several more.

There have been named in all 123 angiosperms (including the twenty-two species, hybrids and intermediate and other forms of *Draba* determined critically by Mrs E. Ekman of Upsala), and it is unlikely that many distinct species were missed in collecting. Again, the six vascular cryptogams recorded are probably all that occur on the island. Unfortunately the same claim cannot be made in the case of the lower plants; August 20th to September 15th is not a long period and, although the seventy bryophytes and seventy-nine lichens probably represent the vast majority of members of these phyla occurring generally on the island, the algae and fungi were not so carefully collected, although certainly they were less numerous. Moreover, many of those brought back have been impossible to name, because of the poorness or insufficiency of the material.

The fresh-water and marine algae named number thirty-one if we exclude diatoms, and the fungi according to a rough determination were twenty-seven, although actually a larger number occurred among the conspicuous types alone. There have been named only six fresh-water diatoms, though all these occurred in large quantities, but in the marine plankton and a little benthic material as many as forty-five species of diatoms were identified, and four other protistoid organisms.

The total named flora from all phyla is thus 391, of which some 305 live on land but only 129 are vascular plants. Critical determination after further collecting might add several to this last number, especially in the genus *Salix*.

Thus several apparently different forms of "*Salix arctica* Pall." could often be collected from the same habitat, while other types which showed a wide range of variation on the island, and sometimes even in contiguous plants growing under apparently identical conditions, were *Cerastium alpinum* L., *Saxifraga oppositifolia* L. and *Silene acaulis* L. These are all known to vary considerably, but on the other hand there appeared to be several distinct species of *Taraxacum* and *Pedicularis*.

RECOGNITION OF HABITATS.

With the almost universal poorness of the vegetation, and the dominance or importance almost everywhere of but a few familiar types, it was obvious that early classification of the plant communities would be impracticable. For, except in sheltered valleys and marshy depressions with a good covering of snow in winter, the vegetation is remarkably uniform—generally a sparse open community of *Dryas integrifolia* with associated willows and saxifrages on the plateau, where puny monocotyledons with the grass habit may occur, and a few tiny ericaceous ground-shrubs. There are hardly any plants of more than a few inches high anywhere on the island and none exceeding a foot. The floristic composition and life form being so uniform it seemed that the best method of working the area in the short time available would be to try to delimit and describe the various habitats with which the vegetation *did* change. Only thus could be obtained a clear impression of the island and its vegetation as a whole—a picture which would be completed when the relative importance of the various habitats (as occupying greater or lesser proportions of the area) could be recognised.

To such ends the author spent the first few days in exploration, and was soon able to draft a rough list of all the main and some of the special habitats on the island. On Akpatok it was the physical features rather than changes in the meagre plant covering that struck the observer; the cliffs and ravines are topographical changes in aspect so overwhelming as to make almost unnoticeable the differences between their own barrenness and the already poor vegetation of adjacent areas. For these reasons the treatment by habitats has been adhered to as being likely to give the most vivid general picture of the island and its vegetation. In the completed classification there are twelve main headings, generally illustrating topographically different habitats which cause the vegetation to change appreciably. These twelve headings afford the chapters of this communication and are listed on pp. 348–9, together with the numerous subheadings to the sections within the chapters.

METHODS OF WORK.

The habitats having been recognised, each was considered separately. There was less than a month in which to work out the whole area, and much of this time had to be spent in exploring, hunting and camp activities; also in general collecting, to obtain as nearly as possible a complete flora of the island. Therefore no intensive work was possible, but, although little more

hot 6 Monotonous gently undulating plateau (p 340) Gleaming
hite limestone relieved by dark patches of vegetation (p 341)

Phot 7 Watercourse on plateau dried up in late summer
(p 342) Well vegetated marginal beaches on right

Phot 8 [illegible] which start watercourses in heads than a primary survey could be carried out, the methods employed seem to give a fair idea of the vegetation, and of the corresponding ecology.

Between them the habitats that were listed cover the whole island, so far as could be ascertained, and their description in each case included lists of species, photography when the weather permitted, and general investigation of soil, water, aspect, and so on. The listing was always of the quick bird's-eye type which emphasises relative importance rather than exact composition, and in virtue of this may give a still better idea of the vegetation. Experience in discrimination, and care in eliminating the personal factor are necessary, and even then it is often difficult to assign frequency-degrees to the bryophytes and cryptogams, in spite of much ground grovelling among these smaller plants. It was found best to consider first the entire angiosperm population of a typical area of the habitat, attempting to give the same significance to the frequency-degrees in all the different habitats, and afterwards to list the lower plants, whose frequency-degrees, where given, have a very different value from those of the angiosperms and pteridophytes. Thus a rosette plant or other angiosperm of average conspicuousness dotted at intervals of from 1 to 3 yards would be called f., whereas an insignificant little lichen so spaced might be called r.

In collecting it was more time-saving to take specimens of all ecologically important types mentioned in the lists, wherever there could be the slightest doubt as to their identity, than to attempt to identify them in the field or in camp during the short time spent on the island. This may not apply to countries whose plants are less easily dried, but on Akpatok it was even better to collect a plant over and over again than to refer it back to an earlier specimen in the presses, and in any case abundant material was wanted for the museums. To save time in writing labels and stowing specimens a method adopted the year before on a hurried trek through Lapland was employed, of frequently collecting specimens into bundles (envelopes in the case of mosses and lichens) tied up with a common label so long as the plants could be described separately in the notes, or given temporary (but definite) names. Arrived back in the museum, the plants are separated and placed on sheets of paper, a new number being given, on a separate label, to each individual plant. This new number is written in ink against the old number or other reference in the notebook (originally all in lead pencil, the only safe writing medium) and the specimens can then be sorted and consigned to the specialists. Lists are returned, and the names interpolated in the original notes alongside the numbers.

ACKNOWLEDGMENTS.

The author wishes to thank the many private individuals and bodies to whom he is indebted for the very existence of this communication. Firstly the expedition (to whose members the heartiest thanks are due for help in numerous ways[1]) was another of the fine efforts of the Oxford Exploration

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[1] Particularly to Mr Reynold Bray of Balliol College for taking many of the photographs, and for helping me to take many more.

Club, and was assisted financially by the Royal Geographical Society, the Royal Society and the University Chest; while the author was assisted by grants to the expedition from Christ Church and Magdalen College, to which Societies he would again tender his special thanks.

The British Museum were most generous in the loan of plankton nets (one from the *Discovery*), bottles and other collecting gear, for which Dr Calman, F.R.S., and the late Mr Alexander Smith of the Zoological Department must both be thanked, while the author's very warmest thanks and tokens of esteem are due to the staff of the Botanical Department for their identification of specimens and other tireless help; he can only hope that they have been in part repaid by finding the material not unattractive and being presented with most of it. The author is indebted to almost every member of the department, but more especially to the keeper, Mr Ramsbottom, to Messrs A. J. Wilmott, A. W. Exell and Geoffrey Tandy for advice, and to the following ladies and gentlemen for their identifications: Polypetalae, A. W. Exell; Drabae, Mrs E. Ekman (Upsala); Apetalae and Sympetalae, G. Taylor; Monocotyledons, J. E. Dandy; Pteridophyta, A. H. G. Alston; Musci, W. R. Sherrin; Lichens, Miss Annie Lorrain Smith; Algae, G. Tandy; Diatoms and Protista, N. Ingram Hendey.

The fungi were determined unofficially in the museum, and no responsibility is taken for such specific names as are given.

In conclusion it is a great pleasure to thank Prof. A. G. Tansley, F.R.S., for the keen interest he has shown in this work, for his careful supervision of the preparation of the manuscript, and for his friendly guidance and helpful criticisms.

HABITATS AND SPECIAL COMMUNITIES.

Abbreviated title or description[1]		Chief feature of most typical vegetation[2]
I. HILL-TOPS: 600 to nearly 1000 ft. ...	350	
(*a*) Of large limestone splinters ...	350	Barren, or a few crustaceous lichens **(1)**[3]
(*b*) Of detritus including soil ...	350	Many crustaceous lichens
(*c*) Less exposed, with polygons ...	351	Angiosperms very sparse (*Dryas*, *Salix artica*, etc.) **(4)**
II. PLATEAU: frost-shattered limestone ...	352	Abundant angiosperms covering about one-eighth of the whole area:
(*a*) Polygons, composed of:	352	
(1) Polygonal areas ...	360	Barren, or with a few herbs
(2) Intervening tracts ...	361	Very abundant *Dryas*, *Salix*, etc., may completely cover these **(6)**
(*b*) Non-polygon, various types ...	363	Angiosperms sparse to closed (*Dryas*, etc.) **(2)** **(5)**
(*c*) Peculiar areas, various ...	366	Including closed grassy or sedgy depressions **(7)**
III. SCREES AND OTHER SLOPES[4]	367	
(*a*) Partially stabilised screes ...	367	Various shales, angiosperms including *Salix* in strips **(3)**

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[1] The number placed after each habitat refers to the page in the general text on which its description begins.

[2] The terms used are purely relative, having nothing to do with the frequency-degrees used elsewhere.

[3] These numbers in brackets and heavy type after the abbreviated vegetation description (right-hand column) are explained and used in Part II (**21**). They also indicate that the community belongs to the more important or distinct communities of the island.

[4] These are placed in the order of their importance as occupiers of relatively greater or lesser areas on the island.

(b) Unstable screes, jagged parts	370	Barren, or a few crustaceous lichens
(c) Dry stabilised slopes	371	Rough, abundant *Dryas* etc. in tussocks, and lichens
(d) Damp slopes with soil patches	372	Sparse herbs—*Oxyria*, Saxifragae, etc. (**19**)
(e) Slopes with wet earthy tracts	373	Very late snow, largely barren
(f) Sandy slopes	373	Binding angiosperms, chiefly *Dryas* patches (**12**)
(g) Earthy screes	375	Very sparse angiosperms—*Salix* and grasses
IV. RAVINES: traced from plateau to sea	376	Beds generally barren, sometimes sides also
V. VALLEY SIDES: sheltered	377	
(a) Damp, snow-covered in winter	377	Dark with vegetation, often closed (*Dryas*, *Cassiope*, etc.)
(b) Drier slopes, no snow covering	379	Richer than plateau, irregular *Dryas*, etc.
(c) Meadow-like areas	380	Sometimes closed grassy vegetation
VI. VALLEY HEADS AND DEPRESSIONS	381	
(a) Lake marginal zonation	381	Variable, sometimes closed beds of Eriophora (**24**)
(b) Boggy dips without lake	382	Closed Eriophora, *Carex* or grasses (**25**)
VII. AREAS WITH VEGETATION DETERMINED BY SNOW (melting season important), 383		
(a) Swallow holes, vary with snow cover	383	Barren to *Taraxacum-Oxyria* tangle (**26**)
(b) Late snow patches	385	Closed zones (*Cassiope*, *Salix herbacea*, etc.) (**27**) (**28**)
(c) Persistent snow patches	389	Barren near the snow, then moss mat and angiosperm zones (**22**)
VIII. ERRATIC BOULDERS: dark and acidic	391	
(a) Exposed, on plateau	391	Lichen half cover—adjacent limestone bare (**15**)
(b) Sheltered, with snow covering	392	Stages in colonisation—lichens to closed mosses with angiosperms (**16**)
(c) In stream bed, varied exposure	393	Barren to almost closed lichens
IX.[1] SPECIAL LOCALISED COMMUNITIES	1	Vegetation always closed and relatively luxuriant—hence notable
(a) Herb areas	2	Species generally much mixed
	2	(1) Non-grassy, herbs dominant (**13**)
	2	(2) Grasses dominant (**14**)
	4	(3) Wet herb-moss mat (**20**)
	5	(4) Dry herb-lichen mat (**8**)
(b) Heath areas, snow covered, local	6	Close dark peaty surface, very dwarf shrubs 2–4 in
	6	(1) *Empetrum* dominant (**9**) (**10**)
	8	(2) Dry *Cassiope*-lichen mat (**11**)
	9	(3) *Salix*-moss mat (**21**)
(c) Thick moss mat	10	Various (snow patches, bird-cliffs, etc.)
(d) Marshy areas	10	*Carex* or grass bed, dark and humous
(e) Hillock tundra areas	11	*Carex*, grass or mixed heath
X. SPECIAL LOCALISED HABITATS	12	
(a) Acidic moraine accumulations	12	Dark, generally closed vegetation much mixed (**17**) (**18**)
(b) Bird-cliffs: increased N at tops	14	Thick moss-lichen mat, generally with angiosperms (**29**) (**30**) (**31**) (**32**)
XI. FRESH-WATER HABITATS	19	
(a) Standing pools	19	
(1) Dried-up beds	19	Centre barren, margin colonised by grasses
(2) Temporary tarns	20	Variable vegetation or barren
(3) Permanent lakes	20	Variable: a few aquatic angiosperms or algae (**23**)
(b) Running streams	21	Variously vegetated; marginal beaches better
(1) Dried-up beds	22	Generally barren
(2) Occasional appearance with pools	22	Generally barren
(3) Free running all summer	22	Variable: a few algae in water
XII. MARINE HABITATS	24	
(a) Brackish water lagoon	24	Filamentous algae may cover bed
(b) Salt water	25	
(1) Recent shingle	25	Very occasional angiosperms above tide limit
(2) Intertidal zone	27	Largely barren, small algae in pools
(3) Plankton and benthos	29	Abundant diatoms and big Laminarians

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[1] Nos. IX to XII will be described in "The vegetation of Akpatok Island. Part II" (21) (in proof for the next issue of this Journal), and the references given after their habitat titles are to pages in this second part.

I. HILL-TOPS.

Many of the hills of the island rise to over 800 ft., while a few reach nearly 1000 ft. above sea-level. In one or two cases they are of acid-weathering morainic material (see Part II), but generally they are of pure limestone. The most exposed tops are almost entirely bare, being shorn of vegetation by desiccating winds and exposed to other difficult conditions, but if we include some less extreme examples we may recognise the following types of surface, each of which shows transitions to exposed scree and plateau formations:

(*a*) Barren limestone splinters.
(*b*) Fjaeldmark[1] including larger limestone blocks supporting some lichens.
(*c*) Polygons.

(*a*) *Barren limestone splinters.*

The most exposed hill-tops have surfaces composed generally of small (i.e. 2 or 3 in. long) limestone flakes and splinters. These may be anything up to 6 in. in length, but are often remarkably constant in size over localised tracts of the area. If they remain as flakes of rock and are not weathered down to soil, the smaller the fragments are the more barren the area will be, though the surface becomes relatively static with the fragments packed tight by the wind, for any loose flakes are sifted in among the others or blown away. In one place where the surface consisted of flakes sharpened into cutting edges by blizzards which moreover eroded their surface and made them rough, and packed them so that they mostly pointed upwards, not a plant could be found even after a detailed search over many square yards; even a small erratic was quite barren. There is no winter snow covering and even in summer the situation is almost continually very windy, or else fogbound. Another difficulty must be lack of water due to fast drying and porosity; but in most examples very occasional crustaceous lichens could be found, chiefly *Lecidea lapicida* var. *ecrustacea*. In some cases of less extreme exposure, where the splinters may be large and smooth, the "black bobble" apothecia of this lichen are quite frequent, while one or two tiny dwarfed Drabae may be met with but generally no other phanerogams.

This barren, wind-smoothed type is most frequently found on the north to west-facing higher slopes, where these meet the strong north-westerly gales which are so prevalent over most of northern Canada and the Labrador Peninsula.

(*b*) *Fjaeldmark including larger limestone blocks.*

Both in their somewhat better vegetation (though this may still consist of little more than a few crustaceous lichens) and in the occasional small patches of earth which may occur on their irregular surfaces, the hill-tops with larger limestone blocks strewn about among the finer frost-shattered particles are an advance on I (*a*) and approach I (*c*). While heaps of splintered rock may occur, the hill-top is generally eroded and smooth rather than rocky, with the contour irregular locally because the surface is strewn with limestone fragments which seem to be more quickly frost-shattered but less eroded at the surface than the flakes in I (*a*). The surfaces of these fragments are smooth and better colonised by crustaceous lichens, remaining whitish or yellowish instead of dark grey and rough. The material is best termed "mountain-top detritus."

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[1] Stony desert of rock debris of all sizes, including some finer soil. In this case it is "Mountain-top detritus" (see *Types of British Vegetation*). However, many fjaeldmark areas have their surface largely composed of bare patches of finely comminuted soil.

Lecideae are again the chief lichens, though small crustaceous Lecanoraceae may occur. Cetrariae seem to be absent—there is not even any *Cetraria nivalis* on the occasional better patches of vegetation—and this may well be due to the extremely windy situation: gales which can cause truckling[1] if not bodily uplifting of rock particles could surely do likewise with the feathery squamules of these poorly attached omnicolous lichens.

With the better supply of water there are few larger limestone blocks, and most of these are flaked flat with the surface on which they lie. On the other hand there is to some depth a considerable admixture of finer soil particles, and where these are aggregated into tracts suggesting the beginnings of polygon formation, there may be occasional patches of higher vegetation[2]. These patches are small and generally consist of a single bushlet of *Salix arctica*, rising no more than an inch or two above the surface, but probably holding some snow in winter. Sometimes there may be a piece of hardy *Dryas* in the patch but the only other angiosperms are forms of *Draba*, and they are by no means constant in the association. Mosses seem to be absent except for *Grimmia apocarpa* Hedw., and in the chief example investigated there were not even any light-coloured "crumbling" lichens such as *Ochrolechia*.

(*c*) *Polygons.*

Small polygons with vegetation much poorer than that occurring around those on the general plateau (see p. 352 *et seq.*) are the main feature of the surface of the more extensive and flat-topped inland hills and ridges. The tops are generally not so high above the surrounding country and always have areas less rigorously exposed than in the previously described types, if only by virtue of their being on a flat instead of a rounded top, or on the relatively sheltered southern instead of on the north-west side.

The polygons chiefly occupy these less exposed areas, and may be either well marked or of doubtful delimitation; in either case their vegetation is very poor, while in somewhat more favourable areas it passes gradually into facies of the ordinary plateau type.

Dryas and *Salix arctica* (often the dwarf form) are the only constant species of these bleak hill-top polygons, though *Polygonum viviparum* is often very frequent, and Drabae and *Saxifraga oppositifolia* may occur. Many of the polygon edges are entirely devoid of higher vegetation, which in the area listed below was limited to patches of *Dryas* and *Salix arctica*. In the patches grew:

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[1] I.e. irregular movement on a surface, more particularly down a slope.

[2] See plate facing p. 170 in *The Isle of Auks* (2).

ANGIOSPERMS		MOSS	
Polygonum viviparum L.	f.	Grimmia apocarpa Hedw.	
Saxifraga oppositifolia L.	o.-f.	LICHENS	
Drabae, barren and dwarfed	r.	Ochrolechia tartarea var. frigida Kbr.	a.
Saxifraga aizoides L.	r.	Cetraria nivalis Ach.	o.

Even here we have on any erratic body of schist, contrasted with the occasional crustaceous lichens (chiefly *Lecidea* spp.) of the larger fragments and blocks of limestone, an abundance of mixed *Lecidea* spp. and *Rhizocarpon geographicum* var. *atrovirens*; while a larger boulder supported even *Gyrophora hyperborea*, and had in its shelter a good growth of *Cetraria nivalis* and *Ochrolechia tartarea* var. *frigida* on a large clump of mixed *Salix arctica, Dryas integrifolia* and *Saxifraga oppositifolia*.

II. PLATEAU.

(*a*) *Stone polygons.*

Almost the whole of the interior of the island is made up of plateau undulating gently between the altitude limits of 500 and 800 ft., embossed by slight hills and ridges which in a few cases exceed 900 ft. In fact, except where slight depressions afford somewhat better shelter and water conditions, or where valleys and deep ravines have been worn by the action of water, the whole of the island is covered by these monotonous barrens. First and foremost, as occupying by far the major portion of the plateau, and thus of the island, must be mentioned the limestone "polygons."

The ordinary types of "stone polygon" have been described from different northern regions by a number of writers, among whom members of the Oxford expeditions to Spitsbergen are notable, especially Huxley and Odell (**3**) and Elton (**4**). This type of surface formation seems to vary more with climate than with the soil or its parent rock, and the limestone polygons so prevalent on Akpatok appear to conform fairly well with the main type in Spitsbergen[1]. The general features and scale of magnitude are indicated in the diagram (Fig. 3, p. 341) and Pl. XXX, phots. 10 and 11, which show the differentiation between the polygonal (sometimes circular) areas and their intervening tracts. The polygonal areas are of finely comminuted soil or clay[2] (on Akpatok always derived from limestone), which is close and compact and often wet right to the surface even in September. The intervening tract is of loose stones, generally with some gravel[3] but little fine soil. It may include boulders a foot in diameter, but even where the fragments are all comparatively small the surface may be raised several inches above the level of the polygonal area, which is generally convex.

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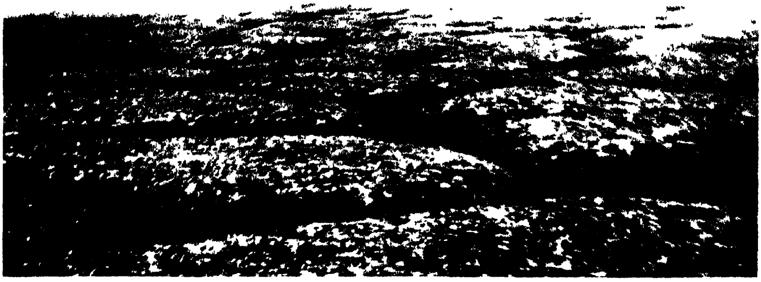
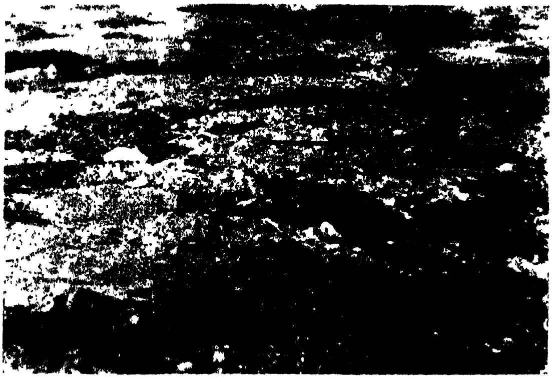
[1] On recent journeys over several parts of Spitsbergen the writer was able to confirm this view, although in general comminution has proceeded farther and the polygons are not so universal and well delimited as on Akpatok, even where the area appears flat and favourable for their formation. The writer has seen very fine polygons on the higher mountains of Norwegian Lapland.

[2] "Mud" when wet—the words are used in the physical sense and imply an apparent preponderance of particles less than 2 μ in diameter.

[3] Again in the physical sense—fragments a few mm. in diameter.



Phot. 9. Giant "tundra polygons" above the bird-cliffs, about 7 yards in diameter, covered by the lush cryptogam "patchwork quilt" (p. 354).



Phot. 10. Typical "stone" polygons on the plateau, with well vegetated intervening tracts (pp. 352 *et seq.*).

Numerous theories have been advanced to explain the sorting of particles of different sizes and other phenomena necessary to give these extraordinary structures. For structures they are, rather than surface features—the stony tracts are continued underground to a depth of 1–2 ft., after which the fragments tend to become smaller before the surface of unweathered limestone is reached (the soil on Akpatok rarely seems to be more than about 3 ft. deep), while the polygons themselves are of compact mud, more or less wet beneath the surface. It used to be said that "polygonal markings" were due to stones falling into the cracks formed when mud dried, and more recently running water and the swelling of mud on imbibition of water have been cited as possible main agents, but it now appears certain that the alternate freezing and thawing in a cold climate is the chief cause.

Huxley and Odell (**3**) have combined the theories of Högbom (**5**) and Nansen (**6**) into a very feasible scheme which, with certain additions to explain further phenomena, may be summarised as follows. Rocks in the Arctic are rapidly split into pieces of all sizes by the expansion of water on freezing. This frost-splitting will be more rapid in hollows where moisture lies (Nansen), and such differential comminution will be self-reinforcing, for the finer the material becomes the more it will take up water by capillarity and the more violent will be the frost action. The action starts in live rock or collections of stones such as are left by retreating ice, and when comminution has reached a certain degree the sorting by "lateral thrust" advocated by Högbom comes into play—an area with fine material imbibes water and expands on freezing, pushing out the material at its edges. When the mass thaws the resulting contraction causes the finer material to be sucked back, leaving the coarser fragments at the periphery. This peripheral region of larger stones, soon becoming the "intervening tract" between two polygons, when properly differentiated will conduct heat better, melting the adjacent mud mush and forming a gutter in the frozen soil or ground ice, at least in the early summer when this is near the surface. The tracts form a network, and so must the accompanying gutters, for water to flow through. When this stage is reached further comminution will be very slow, for the polygons are already composed of fine mud and the intervening tracts will have their stones well drained and thus rarely split by frost. The polygon system may be relatively stable, but is probably only a stage in the weathering of the flattish surface of Arctic soil on which it is formed.

On the porous limestone of Akpatok it is obvious that the presence of water is even more important than the severity of local climate in the processes of comminution and polygon formation, for where drainage is good, as on the edges of cliffs, there is little really fine soil material. There is more on flat-topped hills, where the rough beginnings of polygon formation may be seen, and most of the flatter areas of the plateau seem to have reached the relatively static stage of well-marked polygons further delimited by vegetation in the manner to be described below (see Pl. XXX, phot. 10). The best polygons are encountered in damp depressions and by the sides of lakes, a magnificent example being shown in Pl. XXX, phot. 11; but nowhere on Akpatok does the final stage of comminution to homogeneous mud (often having the surface divided on drying into roughly polygonal areas separated by cracks[1]) seem to have been reached, unless it be in the peculiar area shown in Pl. XXX, phot. 9. This occurs at one point at the top of "Hell Cliff," by the north-eastern point of the island where the cliff is over 600 ft. high—the highest cliff on the island. The giant polygons shown average about 7 yards in diameter and stretch back some 80 yards from the edge of the cliff—the skyline in the photo, along which a polar bear is running. They are vegetated by the lush patchwork quilt described in Part II, for this is a bird-cliff area. And though the cliff-top, before it was rendered humous and retentive of water by this peculiar vegetation depending on the proximity of the nesting birds, must have been well drained, the polygons now go right to the edge, as is seen in Pl. XXXI, phot. 13, of the dip between two of them, which has been further hollowed by the bear who made his lair overlooking the sea.

The domes of the giant polygons are vegetated by the drier type of bird-cliff tundra, and the intervening dips, often nearly 2 ft. deep, by the damper type dominated by mosses[2]. The surface is of fine humous soil, but unfortunately the polygons were not investigated further; nor was any such structure observed in the bird-cliff areas elsewhere. It may be that after emergence from glacial conditions the adjacent cliff was the first to be colonised by nesting birds, and that the resulting plant covering hastened comminution of the surface rock to mud in this most exposed part of the island. They may be true "mud fissure" polygons overgrown by vegetation and "fossilised," but seem more likely to be a peculiar small type of the "tundra polygons" described by Leffingwell (**8**) from Alaska. These average 15 m. across and, according to Leffingwell, arise in winter by cracking, due to contraction with the cold of a severe climate (**9**). Loud reports are heard from the ground in winter and the cracks fill with water which freezes, the resulting wedge of pure ice—seen in the side of one example on Akpatok (**2**, p. 175)—growing year by year and elevating the polygon. It seems probable that here, and here alone on Akpatok, the soil is deep and bears a thick layer of humous muck on top, due to the long-continued influence of the nesting birds.

To return to the stone polygons: several types were encountered on Akpatok, including single isolated patches of fine soil delimited by stone circles and indicating that such structures can be made from single centres, and polygons whose surfaces were made of uniform-sized gravel or even stones, the intervening tracts being distinguished by their stones being up-ended and generally larger. Additionally, some polygons showed various special features

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[1] Cf. various writers, including those cited and Huxley (7).

[2] See X (*b*) in Part II.

Phot. 12. Port Burwell on the mainland of Ungava Bay. Expedition ship *Young Harp* in harbour. The rocks are acidic and most habitats more sheltered, so that the vegetation is very much more luxuriant than on Akpatok (p. 344).

Phot. 13. Polar bear's lair overlooking the cliff; the sea is 600 ft. below. The lair was made by further hollowing the dip separating two giant "tundra polygons" (p. 354).

POLUNIN—AKPATOK ISLAND

which do not seem to have been observed elsewhere. Seven varieties of such features are described below.

(1) *Intervening tracts whose main substance is made of wet mud* into which the feet sink, though the surface includes many coarser, gravelly particles. Such polygons occur in especially damp depressions where frost comminution has almost reached the complete mud stage of uniformly small particles, but they do not belong to one of the usual types of mud-fissure polygons. The intervening tracts are very markedly convex, and though generally narrow are often raised (by lateral pressure exerted by the polygons?[1]) as much as 10 in. (25 cm.) above the periphery of the polygonal area, which in such cases is often almost circular. Such tracts are not "well drained by subterranean gutters" even if these latter exist, which seems improbable in this case, having regard to the semi-fluid nature of the surrounding material. Some other explanation of the convexity of these polygons seems required in place of that of Huxley and Odell, who said that it was caused by better drainage near the gutters, and removal of fine particles from there by the outflowing water. This seems possible for the ordinary stone polygons which on Akpatok are flat except for slightly down-curved edges[2]. But these polygons with muddy intervening tracts are developed precisely in the slight but wet depressions which can be little if at all drained, and it is just these polygons which exhibit the greatest convexity of all! (Cf. Pl. XXX, phot. 11, of an intermediate type with stony tracts with much mud below.)

(2) *Some dry stony areas may have irregular polygons in which the intervening tracts are definitely lower than the surface of the polygons*, which are still only slightly convex, being flat except round their edges. More rarely this occurs with regular, well-formed polygons in damp areas which were probably once dry, for comminution has not gone so far as in most wet depressions.

(3) *In many places the particles near the periphery of the polygon are of an intermediate coarse sand or gravel size, while in some there is, on the surface at least, a grading of particles so that the size decreases constantly to the centre of the polygonal area.* This occurs in drier places and seems to obviate one of the main objections to Högbom's theory of lateral creep, whose sorting effect may be intensified by the increased drainage and removal of the finer material from the sides of the polygon and down the stony intervening tracts.

(4) *Where the surface of a polygon is compact and hard in late summer its edges often show fresh radiating marks, and the centre concentric circles of material of different texture and colour.* The surface is thus like the mud fans of an alluvial delta, suggesting that even if the whole structure was not dynamic

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[1] This is further suggested by the folding of the surface near the periphery in some cases, cf. **Huxley** and **Odell(3)**.

[2] This curvature they may lose in the rare instances in which they have their working hindered by vegetation and are stabilised.

earlier in the season some water flowed off the edge. This may well have been more than was produced by the melting of what little snow rested there.

(5) *Sometimes a large part of the centre of one of the particularly convex polygons of damp depressions seems to have sunk,* and sunk even more than would be the case on partial drying of the surface layers, *to leave a ridge which in some cases may go all the way round.* Unfortunately no photographs of such a feature were taken, but there appears to be an example of a ridge towards the right-hand side of the polygon on the right of Pl. XXX, phot. 11.

(6) *The "umbilicus" or little heap of stones observed by Huxley and Odell* (**3**) *as sometimes occurring in the middle of the polygonal area in Spitsbergen polygons was frequently seen on Akpatok, where its place was in some other cases taken by a little patch of uniformly fine mud.* There were sometimes in these polygons (and sometimes in others without umbilici) small secondary cracks filled with stones (presumably by the action of wind, water and gravity, but with such surprising regularity as to suggest some other motive force) and delimiting irregular secondary polygons within the ordinary mud centres, while still smaller cracks, probably made on simple drying of the secondary polygons, may delimit tiny tertiary ones.

(7) *Sometimes the stones in the centre, instead of forming a raised umbilicus, lie in a slight but well-marked depression,* a good example being visible in the left-hand polygon in Pl. XXX, phot. 11, again taken purely by chance. More rarely there is a little crater of the ordinary mud of which the polygon is composed, the surface being like a decapitated volcano, and there seems little doubt that the significance generally given to the umbilicus, viz. that it is merely the meeting place of the cracks delimiting several secondary polygons, is erroneous. There seem on Akpatok, at least in depressions where moisture is abundant and lasting, to be further complications arising from the expansion on freezing; besides the lateral thrust, which may result in the creeping of stones, and by squeezing the intervening tract cause its fragments to stand up-ended and its level to rise considerably when it is muddy, there seem to be active movements taking place in the centres of the polygons themselves.

The increase in volume of water at 4° C. (maximum density) on freezing is approximately 10 per cent.; hence the very considerable lateral thrust when the polygon centre is saturated. Where the tendency to lateral movement cannot be satisfied by compression and raising of the intervening tract, the pressure in the vertical plane must be intensified, and in that the bottom is of solid rock or frozen soil (as opposed to the pure ground ice mentioned on p. 354) the movement must be upwards.

Thus with the first severe frosts in late summer we conceive of the top of the polygon being frozen quickly, the layer of hard frozen mud getting thicker by gradual extension downwards. Though no ground ice or frozen soil (*tjale*) was observed before the rock was reached at a depth of about 3 ft., the soil temperature fell rapidly until it was only just above freezing-point in the soil overlying the rock. Even if this frozen soil or rock at the bottom cannot extend upwards and intensify the effect until the temperature drop can be conducted from the atmosphere down some already frozen tract, the material in the centre of the polygon will be compressed between the two hard layers as freezing extends downwards from the surface, and will presumably have its more liquid matter thrust out to the sides, since the top of the polygon is heavy and frozen hard. Nevertheless part of the pressure may be expended in raising the level of the surface of the polygon.

It is presumed that freezing extends downwards from the surface rather slowly even if the temperature of the atmosphere is low, for the centre of the polygon is well insulated against the temperature drop and furthermore is of close grain and under pressure. Meanwhile the lateral expression of "juice" will continue and saturate any possible space between the polygon and its intervening tract[1] (or flow between the stones in the case of ordinary polygon areas whose tracts do not contain any mud), until the time will come when the temperature drop has been conducted down the intervening tract and it freezes solid below, together with the adjacent sides of the polygon, and very soon the base, where it abuts on already frozen soil or cold rock.

There are now two surfaces, above and below, extending towards one another, perhaps fairly quickly, and the sides and bases of the polygons being rigid now that they are frozen solid, the only part of the system which can "give" is the surface of the polygon. This, especially in the case of polygons of damp depressions, will arch up further as the core expands on freezing, or sometimes will rupture near the centre where pressure is greatest and give out semi-liquid material. According to Ramann, heaps of fresh soil are accumulated at the surface of many Arctic and sub-Arctic soils in some such manner (**10**).

Next summer, thawing will take place first at the surface and edges and tend to level out any heap of soil passed up the break in the top when freezing took place. Such soil will be fine and very wet, and with the contraction on subsequent thawing of the interior will tend to be sucked down into the centre of the polygon, whose surface layer has elsewhere a greater consistency and possibly in some cases may be hardening by a certain amount of evaporation and drainage even at this early season. Hence the crater or broader stony depression; and it seems that once such a break has been made it will constitute a "weak spot" in any future freezing, especially when coarse material collects in it and no ice can be formed consequent on the better drainage at that point. The domed shape may be kept, material flowing away chiefly at the sides in the manner indicated by the "deltas" and grading of different sized particles at the surface, while the whole structure gives the appearance of being dynamic, with material constantly heaped up at the centre on freezing and to a certain extent sucked back when the core thaws. Meanwhile some of the material passed up may, at an earlier stage in thawing (and possibly in freezing, if the temperature is not low enough to cause immediate solidification), have flowed off the sides and down the intervening tracts, to be sucked back into the base of the polygon later in the thaw.

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[1] The distribution of the vegetation in Pl. XXX, phot. 11 shows that in the more muddy polygons of damp depressions there is in summer good drainage and aeration only at the break between the polygon and its intervening tract. The intervening tract is already saturated, but at its sides occur interstices which will be filled on freezing and emptied again and enlarged with the general contraction on thawing.

Thus there can be a considerable circulation of the semi-liquid matter composing the centre of each polygon, and it is most significant that intermediate or graded particles are only observed on the polygons of relatively dry areas with well-drained stony intervening tracts—through which fine material can be moved by eluviation, and where the early formation of gutters may well be aided by the melting action of running water on ice, as also by more efficient conduction of heat down such stony tracts. The ridges due to the top collapsing are on the other hand only found in the more pronounced polygons of wet places, where no gutters can be formed, and, the bottom being frozen solid (tracts when muddy will be as slow in conducting heat as polygons, and where raised will remain insulated longer), will not allow of sucking in at the sides towards the bottom, so that considerable movement must take place at the top. More significant still, no central umbilicus or crater is to be found in these collapsible polygons.

The constancy in size within certain limits and the regularity in spacing of stone ploygons has never been explained, but it seems that some such conception of the polygon as an actively working unit may be fruitful in future work, which must include observations in the field at all seasons. The polygons are irregular at first, and though the intervening tracts are usually colonised by plants even at an early stage, it seems that on Akpatok this colonisation is never sufficient to stop their being rendered dynamic from year to year, or frost to frost, except in isolated instances on drier areas of plateau[1], and that almost the whole of the surface of the island unless climatic conditions change will in time be reduced to mud, though that will take a long time indeed. At the moment the plants, poor and irregular though they are, seem to be in equilibrium with the soil, which itself has in most places reached this single but long-enduring stone polygon stage in weathering. Climatic and edaphic conditions are so unfavourable that little humus is accumulated even in the intervening tracts, while the polygons are largely bare, dynamic and compact if not always waterlogged at the surface.

As to the degree to which they are dynamic, this must depend on the number of severe frosts obtaining during the period of the year when all is not frozen solid. For six or seven months the ground is continuously frozen to the surface, and in 1931 no frosts were recorded between the middle of August and the middle of September, though they came on rapidly after that. As the climate is very hard, with exposure extreme, it seems possible that there are few complete thaws after the first freezing. Frost comminution may thus take place only a few times in the year, and if this is so it is perhaps not surprising that the surface has not yet been reduced to a uniform mud, if we consider the probable date of the last ice retreat and the number of times a rock surface must be split before it is reduced to clay particles with an average diameter of less than $1\,\mu$.

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[1] And larger grassy areas in the south and south-west, which were unfortunately not investigated.

On the other hand, with many frosts and much water, stones might conceivably move a number of inches in the course of a single year, even to the extent of the unconfirmed observations of Eakin (**11**), who said that a continual "circulation" of large stones up through the centre and down at the sides of the polygon can occur. In this connection it may be noted that a further remarkable feature on Akpatok is the number of sharp splinters and knife-edged stones which somehow stick straight up and cut footwear to ribbons, for they have their other end embedded firmly in the hardened mud surface of a polygon, or in non-polygon fjaeldmark earth (**2**). This up-ended orientation may be the result of lateral pressure and movement beneath the surface on freezing, as is presumably the case with the groups of stones so placed in the intervening tracts in areas where there are polygons; but whether there can be more extensive and directed movement or not, many separate stones even in non-polygon areas seem to be secondarily placed in this manner and not produced *in situ* or left by water erosion.

Remarkable, too, is the frequent phenomenon on even the slightest slopes, where "elongate polygons" or more lengthy strips of stones, alternating with soft material, are produced as a result of solifluction[1]. Generally any steeper slope that is wet is composed largely of finer material, the tracts of stones being shallow and resting in depressions in the muddy surface, but we still seem to be dealing with soils disturbed by frost action wherever there is permanent water. The coarser material is aggregated into separate tracts as a result of the alternate expansion and contraction on freezing and thawing, though here the polygonal arrangement is completely upset by gravity. The sorting of coarser fragments and stones at the surface is a tendency also shown on the plateau, and may well be due to a Högbom creep, functioning vertically and in this case greatly aided by eluviation and gravity.

Sometimes the stones on steep damp slopes are big and jagged, with hardly any mud visible, though all may be soft and wet beneath the surface. This is true of the tops of some slighter slopes, where neither comminution nor lateral sorting into tracts is complete; the stones lie flat and appear to be rapidly split, for their angles are clean and their surfaces smooth, showing no signs of secondary weathering.

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[1] Cf. **Huxley** and **Odell (3)**, also **Eakin (11)**, and see pp. 369 and 373.

As Elton has recently pointed out, these stone polygons and other structures vary greatly with climate in different regions, so that observations and conclusions for one region must not be unreservedly applied to another. In causes and working the wet domed polygons with thrust up muddy intervening tracts and a central depression or collapsible top, may be very different from the ordinary, relatively flat polygons on the plateau of Akpatok Island. These latter show the best alluvial deltas and vary from 2 ft. to 2 yards in diameter, with intervening tracts 6 in. to a foot broad. They cover most of the island and with the various strains set up on freezing and thawing are certainly dynamic at the surface, which even if it is hard and dry in summer is always compact and badly drained and aerated. The soil water is never acid, even under the thickest tufts of vegetation growing on the intervening tracts. As tested by the B.D.H. "Universal" indicator it was generally *p*H 7·5–8·0 at the surface in the wet centre of the polygon and the same 6 in. below, where the soil even in September was sometimes wet enough to flow. This considerable alkalinity is suggestive again of the circulation and other movements postulated, the ground-water continually coming in contact with the atmosphere and absorbing more CO_2 for the formation of $Ca(HCO_3)_2$, with the result that it becomes progressively more alkaline.

In places in the intervening tracts the plants form a dark soil and the *p*H is nearer neutrality, and in some cases *p*H 7·0 was recorded. However the usual alkalinity strongly suggests bad drainage and consequent long and close contact of the water with the limestone. The annual precipitation appears to be small, and this contact is probably maintained, in areas that are not directly drained by rivers or swallow holes, as a result of permanent subterranean ice blocking the joints in the otherwise porous limestone rock. Nevertheless the intervening tracts of polygon areas may in summer be arid to an extent that in some places probably limits plant growth considerably.

One hesitates to draw any further immediate conclusions about these remarkable features of soil structure which, as has already been emphasised, occupy in one form or another almost the whole surface of the island.

The vegetation of ordinary plateau stone polygons.

(1) *The polygon areas themselves.* In contrast with the "intervening tracts" of large rock particles and loose texture, the polygonal areas themselves are very little vegetated and often support no plants at all. Relative instability and poor aeration seem the two chief factors contributing to this result. Though the surface of the polygon in drier examples is often littered with small frost-shattered splinters of limestone, below it is always of closely compacted soil of fine texture, hard and yellow when dry, muddy when wet. Generally it was fairly damp—often very wet below even in the August of an exceptionally dry year—so that aeration for the roots of plants would be poor in the extreme. Nevertheless the roots of the larger Salices growing so well in the intervening

tracts were often found penetrating far into the centre, so that it seems that the relative instability of the surface of the polygon areas may be more important than lack of aeration in preventing the establishment at least of woody types so notoriously tolerant of waterlogging as the Salices, and which at the same time grow so extremely slowly (see p. 362).

However this may be, most polygons are devoid of any sort of higher vegetation. The list of plants given below is composite and collected from many areas. It will be seen that only *Polygonum viviparum* is more than rare, while even the few plants that do occur are generally rooted not in the solid, close-textured general surface but in little cracks which form the boundaries of secondary polygons within drier examples of the large ones. In the broader and older-looking of these cracks stones have collected and these promote drainage.

Any stones filling the little cracks or lying elsewhere on the surface of the polygon area are generally devoid of lichens and mosses, though those listed may occur—always of poor growth and chiefly along the little stony or cracked edges of the miniature polygons.

ANGIOSPERMS

Polygonum viviparum L.	o.-f.	Puccinellia angustata (R.Br.) Rand and Redf.	v.r. (1)*
Saxifraga oppositifolia L.	r.		
S. aizoides L.	r.	Lychnis apetala L.	v.r. (1)*
Alsine Rossii (R.Br.) Fenzl	r.	Draba sp.	v.r. (1)*

* I.e. in an area of many polygons.

LICHENS (all intermittent and of poor growth)

Polyblastia Sommerfeltii Lynge
Lecidea goniophila Schaer.
L. emergens Flot.
Protoblastenia calva A. Zahlbr.

(2) *Better vegetated boundaries between polygons—the "intervening tracts."* Digging in these tracts generally revealed below the rough surface of larger stones a loose, light soil, plentifully admixed with stones which farther down were quite small, giving better drainage than in the polygons themselves, also relative stability and prevailingly dry instead of wet or waterlogged conditions. The result is seen in the plentiful plant covering they often support as in Pl. XXX, phot. 10, showing almost continuous dark lines of vegetation over the intervening tracts. Moreover, just under the better patches of vegetation the soil between the stones may be humous and fairly dark in colour, a friable, well-aerated soil of crumb-like structure, though the limestone is so preponderant that no degree of acidity is ever developed.

In the driest and most exposed areas *Dryas integrifolia* is generally the chief component of these streaks or patches of vegetation, often almost the only plant present; but in the more typical areas listed below, though it formed the centre of nearly all the more stable patches, it was often locally dominated by bushes of *Salix arctica*, while *Carex misandra*, *Saxifraga aizoides* and *S. oppositifolia* were generally frequent (cf. Pl. XXXII, phot. 14).

None of the Salices rise to more than a couple of inches (5 cm.) above the level of the patch on which they are growing. Though even here on the plateau they often creep a foot or more along the ground as little twisted and gnarled stems, their axes are never more than about half an inch in diameter, but may show as many as twenty-five annual rings under the very thick, corky bark. The habit testifies to the severity of the conditions—the winter snow covering may be almost nil owing to the strength of the gales, and in summer insolation is high and the wind desiccating except when the plateau is fogbound. But though the surface of the polygons is doubtless generally blown clear of snow, some must collect around the edges, and this affords protection enough for the Salices with their thick corky rind. Apart from the Salices, most of the plants are of a close cushion form, rounded and compact (**12**).

Even on these plateau barrens the biotic factor is probably of importance in some places. Where growth is so extremely slow, we can conceive (and not infrequently see evidence) of considerable damage being done among the Salices by the polar bears which, marooned on the island when the ice leaves its shores in spring, roam about everywhere in search of their summer vegetarian diet, while in some places the frequent but reduced axes of *Polygonum viviparum* are all stripped bare of bulbils and leaves, a phenomenon explained on opening the bulging crops of some of the numerous migrating—and in a few cases nesting—ptarmigan, which at this season appear to feed on little else.

ANGIOSPERMS		S. aizoides L.	f.
Dryas integrifolia Vahl	a.-d.	Carex misandra R.Br.	f.*
Salix arctica Pall.	f.-l.d.	Salix reticulata L.	o.
Polygonum viviparum L.	f.-l.a.	Carex scirpoidea Michx.	o.
Salix Hookeriana Barr.?	f.	Kobresia simpliciuscula (Wahl.) Mackenz.	r.
S. arctica Pall. (dwarf form)	f.		
Saxifraga oppositifolia L.	f.	Draba sp.	r.

* Tallest plant about 7 in. high.

Though they were not much in evidence, both mosses and lichens are fairly abundant in the patches of vegetation. From these patches the following lists were made:

BRYOPHYTES			
Didymodon rufus Lor.	f.-a.	Grimmia sp.	o.
LICHENS			
Rinodina roscida Lynge	a.	Cetraria nivalis Ach.	o.
Lecidea speirea Ach.	f.-a.	Cetraria islandica var. tenuifolia Wain.	r.
Rhizocarpon petraeum Massal.	f.-a.		
Cladonia pyxidata Hoffm. var.	o.		

The limestone fragments of the barrens are often almost bare of crustaceous lichens, but strikingly different are the occasional erratic stones and small boulders of mica schist left by some old glacier. They are often coloured bright orange by a radial growth of *Rhizocarpon geographicum* DC. var. *atrovirens*, while other lichens they typically support are the following:

Lecidea lithophila Ach.
Verrucaria obsoleta Lynge
Lecanora rupicola A. Zahlbr.

(*b*) *Non-polygon "fjaeldmark" etc.*

Although the *Dryas-Salix* polygons described above are the usual formation covering most of the plateau, there are many regions, especially where the surface is very dry, in which the frost-shattered fragments of all sizes are not so neatly sifted, but are mixed haphazard, giving barrens of loose stones with a considerable admixture of finer soil particles. The nature and sparseness of the vegetation of these "fjaeldmark" areas depend not only on the composition of the surface (which may vary greatly) but also on exposure and other factors, with doubtless a nitrogen problem as acute as anywhere on the island. In spite of these variations a general consideration of the habitat-type will suffice, for the vegetation is poor and almost always has *Dryas* as the chief plant, with some willows and saxifrages associated.

Better vegetated facies may occur on slight slopes where there is some sifting into rough polygons (cf. V(*b*)); but on exposed cliff-tops and in the windswept country behind the vegetation is very poor indeed, for though the surface is smooth and fairly static it is generally composed of small fragments with little intermixed soil. This does not seem to be a stage in the succession to *Dryas* fjaeldmark, since the fragments are already broken down small, and there are no larger ones to accumulate snow in winter and so allow more stable vegetation to develop. The surface soil is close-packed but probably dynamic in the face of great winds, and the binding plants are *Saxifraga oppositifolia*, the only constant angiosperm. This type (i) will be described first, followed by the rough *Dryas* fjaeldmark (ii).

(i) Saxifraga oppositifolia *barrens*.

In marked contrast with the luxuriant moss or lichen mat (see Part II) developed above the bird-cliffs at the north and south ends of the island, most of the other cliffs have their tops and immediate hinterland of rough limestone fragments which are frost-shattered to a small size, sometimes little larger than coarse sand, and packed tight by wind. The most typical colonist is always *Saxifraga oppositifolia*, after which this type of habitat and dependent vegetation has been named. The surface is gently undulating or flat, except where it is rounded off to the cliff edge and may here be entirely devoid of vegetation, as is seen in Pl. XXVIII, phot. 5, of low cliffs and long rounded slopes taken on the west coast.

In the example investigated the limestone fragments were almost uniformly small—generally 2–5 cm. in length—and packed by wind to form a surface which was smooth but crunched under foot. As on the hill-top I (*a*) this brittle nature is due to erosion and solution on the extremely arid and exposed area, the surfaces of the fragments being rough and their bodies thin and sharp, for they are so dry that they remain for a long time without being split by frost, the good drainage also accounting for the absence of polygons from many such areas. Moreover there can be no winter snow covering except in dips, though these occur where small streams cut a lip in the cliff-top. Here drifts accumulate and a good *Cassiope* mat may be developed, with associated *Dryas*, Salices, *Rhododendron* and *Carex misandra*. This community is edged by one of *Dryas* with *Cetraria nivalis*, as in the case of the more extensive "late snow patches" described on p. 385 *et seq*.

The vegetation of the "barrens" under consideration is limited to one or two plants every few feet. These are almost always *Saxifraga oppositifolia*, whose tufts may sometimes be a foot in diameter and harbour small mosses and lichens. Other associated plants are at best occasional and of poor growth.

ANGIOSPERMS			
Saxifraga oppositifolia L.	a.	Saxifraga caespitosa L.	r.
Cerastium alpinum L.	o.	Alsine Rossii (R.Br.) Fenzl	r.
Carex nardina Fr.	o.*	Festuca brachyphylla J. A. and J. H. Schult.	r.
Drabae (include D. groenlandica E. Ekman vel hybrida)	r.-o.	Woodsia glabella?	v.r.

* Chiefly where particles small and surface sandy; cf. sandy screes (p. 374).

The following lichens and mosses occurred in the larger patches of *Saxifraga oppositifolia*:

MUSCI			
Grimmia apocarpa Hedw.		Tortula ruralis Ehrh.	
		Trichostomum tortuosum Dixon	
LICHENS			
Ochrolechia tartarea Massal. var. frigida	a.	Alectoria ochroleuca Nyl.	o.
Cetraria nivalis Ach.	a.	A. divergens Nyl.	
		Lecanora verrucosa Laur.	
		Candaleriella vitellina Müll. Arg.	

The only plants between these patches of higher vegetation, besides the occasional angiosperms, are crustaceous lichens growing on some of the stones:

Biatorella morio Mudd	a.	Rhizocarpon geographicum DC. var. atrovirens	f.
Caloplaca elegans Th. Fr.	a.		

On their under sides the stones are in places green with a Cyanophycean investment.

(ii) Dryas *fjaeldmark*.

In situations farther inland and hence less rigorously windswept, these *Saxifraga oppositifolia* barrens may pass to a rough type of *Dryas* community. The vegetation may be as much as half closed and the area has the appearance of a fjaeldmark, with much intermixed soil and other limestone fragments of all sizes, including larger blocks which project and must accumulate some snow in winter.

These rough fjaeldmark areas are of frequent if limited occurrence in some of the less exposed plateau regions where polygons are not made. In type and flora they may vary considerably in different places, often being interrupted by heaps of frost-shattered rock (frequently produced *in situ* by the weathering of a single block) whose fragments are either barren or show some stage of succession to the fjaeldmark climax of such exposed regions. Below is a list of the species occurring on a typical *Dryas* fjaeldmark area above "Cove I."

Dryas plants of tufted growth form the centre of almost all the tussocks of vegetation and may rise an inch or two above the stony areas between their boundaries, while the subsidiary flora includes quite a number of species, for the surface is broken and the soil often fairly damp, so that it is difficult to say why no polygon formation is shown. The surface is undisturbed, so the more stabilised *Dryas* patches have a thick, dark humous core, though this contains light gritty limestone particles and is neutral or slightly alkaline. Underneath, the limestone soil is stained brown by leaching from the humous clump, while between the patches of more stabilised vegetation come light-coloured areas largely of small particles and not unlike the more open *Saxifraga oppositifolia* barrens. Conspicuous, and contributing to the light grey aspect of the area, is an abundance of *Ochrolechia tartarea* Massal. var. *frigida* and other light-coloured lichens, while the little *Carex nardina* plants growing abundantly on the bare tracts between the *Dryas* tussocks are also grey in colour at this season.

Dryas integrifolia (up to half-covering)	d.
Carex nardina Fr.	a.
Saxifraga oppositifolia	f.-a.
Salix reticulata L.	o.
Cassiope tetragona (dwarfed axes)	o.
Silene acaulis L.	o.
Polygonum viviparum	o.
Rhododendron lapponicum (L.) Wahl.	o.
Salix arctica	o.
Kobresia simpliciuscula (Wahl.) Mackenz. (local)	
Carex pedata Wahl.	
C. rupestris All.	
C. misandra	r.
Saxifraga aizoides L.	r.
Tofieldia borealis (Wahl.) Wahl.	v.r.
Pedicularis sp.	v.r.

Crustaceous lichens are abundant on the stones and the list shows additions to that from the *Saxifraga oppositifolia* barrens, though the larger lichens are numerous in species rather than important components of the vegetation, and seem to be dependent on the shelter and perhaps snow covering behind boulders and the larger patches of vegetation. Both the *Ochrolechia* and *Cetraria nivalis* are, however, abundant; the latter being of good growth indicates that the snow covering is at most discontinuous and early melting.

MUSCI	
Grimmia apocarpa Hedw.	
Dicranum groenlandicum Brid.	
Tortula ruralis Ehrh.	
LICHENS	
Ochrolechia tartarea Massal. var. frigida	a.
Cetraria nivalis Ach.	a.
C. islandica Ach. var. tenuifolia (crispa)	
Cladonia mitis Sandst.	
Alectoria divergens Nyl.	
A. ochroleuca Nyl.	
Biatorella morio Mudd	
Caloplaca elegans Th. Fr.	
C. Jungermanniae Th. Fr.	
Candelariella vitellina Müll. Arg.	
Lecanora epibryon Ach.	
Rhizocarpon geographicum DC. var. atrovirens	

A *Dryas* fjaeldmark of more luxuriant appearance listed near the south end of the island had much the same composition, except that the frequency-degrees of the more important plants were generally higher, while some of the rarer ones were replaced by the only two leguminous plants on the island, *Astragalus alpinus* L. and *Oxytropis podocarpus* A. Grey, which both seemed to be restricted to the extreme south. *Orthotrichum speciosum* Nees was the chief moss, but the lichens were almost identical with those in the list given above, while the soil between the larger fragments (there were no large boulders so the surface was relatively smooth) was still neutral or alkaline, though a darker grey under the more stabilised vegetation. A significant difference may lie in the greater abundance of *Salix* bushes, while a real advance in the succession is to be observed in damper and more sheltered dips. The fragments are all weathered down to a small size, including much fine soil, and the vegetation when once it has stabilised the surface may advance to an almost closed community of *Dryas* tussocks with *Cassiope* and Salices. Carices, Leguminosae, and *Pedicularis* spp. (including the big *P. lanata* Pall. ex Stev.) are much in evidence, while a thicker and continuous *Dryas* mat is often developed as one of the zones behind the bird-cliffs (see Part II), to the special conditions of which its more constant luxuriance must be related.

(c) *Peculiar areas.*

While the majority of habitats, such as hills, ravines, lakes and bogs, which may interrupt the otherwise even monotony of the plateau barrens, are described under separate headings elsewhere, there yet remain to be mentioned the less marked variations from the usual polygons or rough fjaeldmark.

The ordinary plateau types of vegetation may vary very considerably, especially when a slight slope is ascended or a ridge topped. The rougher polygon or fjaeldmark areas become much poorer, often in relation to a less even weathering of the surface fragments, and are interrupted by barren bouldery tracts or heaps of frost-splintered rock. On the other hand, in the slightest of dips a much better facies may be developed, such as the dark tract of vegetation seen under the ridge in Pl. XXXII, phot. 16. Here there must be some snow covering in winter, and the ground may be damp even at a late season; it is generally washed or weathered into a coarse limestone silt or sand, and may support an almost closed community of large grasses (especially *Arctagrostis latifolia* and *Pleuropogon Sabinei* in damper examples and *Deschampsia alpina* in drier) and sedges (especially *Carex membranopacta*, which is almost always present and often abundant to dominant) and sometimes cotton grasses. In many cases there is an almost pure society of one or another of these types, the individual plants often growing up as small tussocks with tracts of bare soil between, and suggesting a transition to the more favoured hillock tundra areas described separately (Part II).

Whole regions of the flat country of the south and south-west of the island are covered with a more or less closed community of grasses, sedges and cotton grasses, with or without Salices and forbs, but the better-vegetated depressions in other parts are either beginnings of watercourses, in which case their water will drain away and the area early become dry and cracked, or they are mere depressions with no outlet for the water which collects when their winter covering of snow melts. In the last the soil remains for the most part wet and supports one of the damper communities, although evaporation may even here leave the *surface* dry and cracked if it is not colonised: other depressions may be drained through swallow holes (see p. 383).

III. SCREES AND OTHER SLOPES.

The numerous dynamic screes and more stabilised slopes on the sides of ravines and the steeper valleys are a great feature of the island. Seven principal types, all of limestone origin, were distinguished, though many intermediate stages occur. They are described in order of importance.

(*a*) *Partially stabilised screes.*

In climates favourable to plant life, unstable screes are maintained chiefly below crags from which fresh rocky material is continually being broken. On Akpatok the type of scree most frequently met with is very different—an even slope eroding over its whole surface, at least where the material is continually being removed from the bottom by water, or by gravity where there is a sheer drop below. The scree, at least when relatively mature, generally extends to the plateau above without the intervention of a rocky crag, and has its component particles secondarily weathered into shale, small stones, and usually a certain amount of finer soil material. Such screes are relatively static and may be walked up with ease, especially where they are colonised by higher plants. Many different types occur, of which perhaps the most familiar is that on slighter slopes with irregular patches of vegetation, and not unlike the poorer, dry valley slopes (V (*b*)). The incline, however, is much steeper, often 35 or 40°, while there is much less soil and comparatively little vegetation. Nevertheless the lists of plants are similar, except that there are few lichens apart from crustaceous forms on the rocks, and the frequency degrees of all the chief plants except *Salix arctica* are lower.

Another type of scree may be well vegetated in some parts though almost barren in others. This is well seen in Pl. XXXII, phot. 15, where the long scree occupying most of the middle of the slope which forms the side of the ravine has its upper end relatively barren, for it is so freely supplied by stones falling from above that the top part is much disturbed. On the other hand the scree on the ridge above has a rounded, relatively stable top which is fairly well vegetated, although the part below is dynamic and barren, for the fragments of rock fall fast and frequently as soon as they are disturbed by the acting agencies—gravity, wind, frost-splitting or heaving, water or prowling animals.

As the great ravines wind their way inland, becoming less deep and finally petering out, their sides tend more and more to become a single uniform scree of this partially vegetated but still unstable type. At first the screes may be 200 ft. or more long and slope straight from the top, especially where water action is continually removing the bottom, but inland they are shorter, often with rounded, relatively stable and mature upper ends. The top may in places be completely stabilised by vegetation, which remains as a dark hump—at least until the rock below is eaten away and the whole falls with a crash.

From such vegetation at the top, the scree below may be well supplied with humus. Hardy and long-lived willows are the main components of the patches of vegetation, which often persist as long strips passing down the slope even where the scree is more dynamic, for the rock fragments moving downwards will slide or roll in the barren depressions between these strips, disturbing only their edges. This accounts for the dark vegetation developed towards the bottom of the middle scree in Pl. XXXII, phot. 15; the top is steep and barren, disturbed by rock fragments hurtling over the crag, but below most of them are carried down along definite chutes, while the few that continue over the slighter, vegetated slopes have lost the momentum of their fall and are relatively harmless, either rolling singly over the vegetated patches or sliding *en masse* down small chutes when their accumulated weight overcomes friction, but again causing little disturbance.

Sometimes vegetated patches may be buried or cut into strips by moving fragments, but on the other hand vegetation on some slopes may act as an apparently complete and permanent stabiliser, with the plants rooted in the soil which accumulates beneath the surface detritus. They bind loose pieces of rock and hold any others which may be piled about the growing patch of vegetation, so that the level rises—if only in relation to surrounding parts from which removal continues—the slope gets less steep in places and in time more static; hence still better vegetated as the process is progressive and cumulative. On the other hand such a system of screes as that seen in Pl. XXXII, phot. 15, with its complicated physiographic processes and potentialities, must be almost perpetually dynamic, at least until its components are merged into one continuous slope and the bottom of that slope is no longer removed by the rush of melting snow water in early summer.

Rocky outcrops with perpendicular cliff faces, which may be dark with vegetation, are sometimes met with on screes. They may be weathered, but do not consist of moving particles which grind against one another.

Another frequent type of scree consists of irregular jagged limestone rocks on slopes which are gentle enough to allow of some degree of stability, or at least to prevent frequent rapid movement. In spite of weathering there may be no soil except that which collects by eluviation and gravity beneath the surface, but though the limestone blocks are for the most part bare they may support occasional cryptogams, the following being collected in a space of a few square yards:

MUSCI
  Hypnum hamulosum B. and S.

LICHENS
  Caloplaca elegans Th. Fr.
  Cetraria nivalis Ach.
  Lecanora epibryon Ach.
  Lecidea goniophila Schaer.
  Protoblastenia calva A. Zahlbr.

of *Hypnum revolutum* Lindb., and in places *Lecanora epibryon* Ach. In this cushion there were rooted small plants of *Saxifraga oppositifolia, Polygonum viviparum* and *Draba*. Pl. XXXIII, phot. 17, shows several such strips, which generally include tussocks of *Dryas* and have unstable fragments of limestone scree disturbing their sides, but manage to hold their own, though in places half-buried beneath debris.

On more dynamic screes occasional shorter, V-shaped patches of vegetation may develop in the shelter beneath small rocky outcrops, or behind large boulders embedded firmly in the surface. Sliding fragments rush past the outcrop but do not disturb the patch of (generally more finely weathered, earthy) material which it shelters, and here alone the vegetation may be closed.

The difficulty of existing on such screes is further indicated by examining the occasional plants of *Draba* which are often the only angiosperm colonists in the more open parts: one specimen of *D Bellii* f. *gracilis* had a root growing down 18 in. (45 cm.) below its tiny rosette and little flowering axis 2½ in. (6 cm.) high, while another plant had been so disturbed by the sliding away of the limestone through which its taproot had grown that its rosette was living a foot below the point at which it had originally rooted, the root lying on the surface with only the tip in the soil.

(*b*) *Barren unstable screes of jagged particles.*

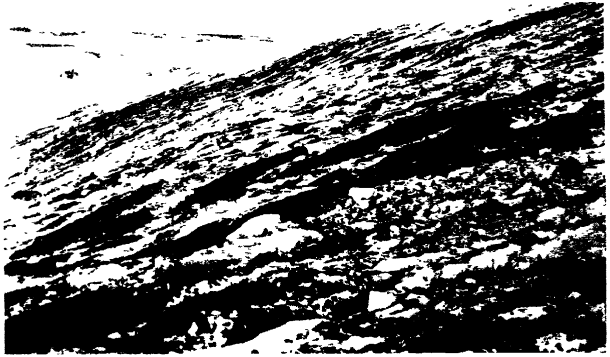
Barren, extremely unstable screes of irregular rocky fragments may be formed wherever a steep slope or cliff is being rapidly weathered, and they persist above, on, or below many such cliffs around the coasts or in the larger ravines. Still more often these very dynamic screes form the sides of small "young" ravines inland, where they may be so dynamic as to be difficult to climb, a whole avalanche of fragments often sliding downwards immediately they are touched (Pl. XXXIII, phot. 18).

Where the fragments are all shaly, weathered and fairly small (say 2–6 cm. in length), there may be no trace of vegetation, though a closer examination generally reveals the presence of one or two tiny crustaceous lichens, whose "fruits" appear as black or orange bobbles on the surface of some of the larger limestone particles, into whose soft and easily corroded substance the thalli have eaten their way with the help of dissolving acids.

Another type of scree covering considerable areas towards the exposed tops of hills is composed of small, sharp, frost-flaked limestone fragments packed tight by wind, which blows away any loose flakes, though otherwise the area may be relatively static. Nevertheless, such a scree generally supports no angiosperms or other non-saxicolous plants but only occasional crustaceous lichens, the surface of the flakes being rough and their substance so eroded that they are brittle and crunch underfoot. *Lecidea lapicida* var. *ecrustacea* was the only plant in evidence on one such area.

Phot 17. Long strips of vegetation extending down dynamic scree. *Salix arctica* the chief plant (pp. 369–370).

Phot. 18. "Young" ravine inland the sides are dynamic screes of irregular limestone fragments (pp. 370 and 376)



Phot. 19 Rough dry slopes largely stabilised by vegetation *Dryas* is the chief plant and the area approximates to fjældmark (pp 371 and 376)

Phot. 20. Herbs on damp soil left by late melting snow (pp. 372 and 388). Above, left to right *Saxifraga aizoides*, *S. caespitosa*, *Poa alpina* and *Oxyria digyna*. Below, left to right *Draba* sp., *Saxifraga cernua*, *Arabis alpina* (fruits behind stone) and a large patch of *Cerastium alpinum*

Even here there are occasional erratic pieces of mica schist, which show immediately how much more favourable for colonisation are the more stable acid-weathering surfaces they provide, for they may be as much as half-covered by crustaceous lichens, chiefly the well-known (**13**) yellow-fruited silicicolous type *Rhizocarpon geographicum*, here mostly var. *atrovirens*.

One more dynamic and largely uncolonised type of slope must be mentioned: a type including large, square-faced blocks of limestone developed as a heap below cliffs (see Pl. XXVII, phot. 2) and fast-weathering crags. The faces of the blocks are generally smooth and bare of any trace of plant life, although in places, where they are neither washed by waves around the shore nor left too late by melting snowdrifts, colonisation may proceed through lithophytic and chomophytic communities of crustaceous lichens and mosses.

(c) *Rough but stabilised "old" dry slopes.*

Various types of more stabilised slope may occur in different situations, but the following example was at an altitude of about 700 ft. above Harp Cove and apparently had some snow covering in winter. It was developed beneath the remains of a rocky crag which had weathered down and was now largely stabilised by vegetation. The incline was too slight for the slope to be actively dynamic when the supply from above ceased: as is seen in the photo (Pl. XXXIII, phot. 19) the material has become weathered into fragments of all sizes, and in places finally stabilised by binding, tussocky vegetation in which *Dryas* is the all-important plant.

The majority of the tussocks of this open vegetation have a plant of *Dryas* forming the centre if not the whole, and a core of dark soil with a high humus content—almost pure humus towards the top of the older tussocks. Topography and the dryness at this season suggest that the water supply is mainly from precipitation rather than percolation from a spring or late melting snow. Altogether it was not surprising to find the *p*H towards the tops of these older tussocks distinctly, though only very slightly, on the acid side of neutrality—about *p*H 6·5 on the B.D.H. capillator scale, using the "Universal" indicator.

The abundance and luxuriant growth of the lichens further indicate the relative stability of the area, which looks dark coloured compared with ordinary limestone slopes or screes—and that in spite of the abundance in places of whitish "crumbler" Lecanoraceae such as *Ochrolechia tartarea* Massal.

The following is a full list—at least of the vascular plants—from a tract about 3 metres broad down some 10 m. of slope, which was here about 80 m. long.

ANGIOSPERMS

Dryas integrifolia Vahl (open community)	d.	Polygonum viviparum L.	o.-f.
Salix arctica Pall. (dwarf form)	f.	Silene acaulis L.	o.
Cassiope tetragona (L.) D.Don. (tufts in higher Dryas tussocks)	o.	Saxifraga aizoides L. (poor growth)	o.
Carex misandra R.Br.	f.	S. oppositifolia L.	r.
C. nardina Fr.	f.	Salix reticulata L	r.
		Draba sp.	v.r. (1)

MUSCI			
Bryum sp. or spp. (barren)	a.	Hypnum revolutum Lindb.	f.
LICHENS			
Ochrolechia tartarea Massal.	a.	Cladonia pyxidata Hoffm. var.	o.
O. tartarea var. frigida Kbr.		Xanthoria (Lychnea) candelaria Arn. (yellow, conspicuous)	r.
Lecanora epibryon Ach.		Lecidea goniophila Schaer. (chief lithophyte)	a.
Cetraria nivalis Ach.	f.		
C. islandica Ach. var. tenuifolia (crispa) (luxuriant tufts on vegetation)	o.		

(*d*) *Damper, less steep* Oxyria *slope.*

Where the slope is fairly static and not too steep, with a lasting supply of ground water (apart from the water supplied by the melting of the snow covering which leaves the surface layers of soil wet), an open community of ephemerals develops wherever a certain amount of soil is present between the larger blocks of limestone. In places small patches of bare earth appear, and may be colonised by quite a number of plants, as is seen in the photo (Pl. XXXIII, phot. 20), though it must be admitted that this depicts a particularly well-vegetated and rather specialised area forming the extensive inner zone of a late snow patch (cf. p. 388).

The plants typical of such slopes generally root in the patches of soil, or in soil which exists beneath the stony covering. This soil is compact and damp, so that the *Oxyria* plants are of good growth and form the main feature of the vegetation. However the plants are only single and scattered, no mat being formed. Another feature of this very sparse and open community is the frequency of upright axes of *Saxifraga cernua* L., with their white flowers and clusters of little red bulbils in the leaf axils.

An area exemplifying this habitat gave the following considerable list:

ANGIOSPERMS			
*Oxyria digyna (L.) Hill. (chief plant)	o.-a.	Saxifraga oppositifolia L.	o.
*Saxifraga cernua L.	f.	*S. caespitosa L.	o.
*Cerastium alpinum L. (good patches, see photo)	f.	*S. aizoides L.	r.-o.
*Arabis alpina L. (fruits in photo)	f.	Phippsia algida (Soland.) R.Br.	r.
*Draba spp. including D. Bellii Holm. and D. oblongata f. ad D. Bellii	f.	Polygonum viviparum L.	r.
Puccinellia angustata (R.Br.) Rand and Redf.	o.-f.	*Poa alpina L.	r.
		Salix arctica Pall. (seedling)	r.
		Carex misandra R.Br.	v.r. (1)
		Lychnis apetala L.	v.r. (1)

* Examples visible in Pl. XXXIII, phot. 20. These late snow indicators are generally open soil plants.

Quite remarkable is the number of Linnean species of alpine and northern regions of the Old World which grow here under the better conditions of good snow covering and plentiful water supply—though the water is always neutral or alkaline and the growing season very short where the snow melts so late.

Mosses are little in evidence, though at least three species occur, while the only lichens are crustaceous and saxicolous, for the soil is wet.

MUSCI		HEPATICAE
Hypnum polygamum Schp.	r.	Fimbriaria sp.
H. revolutum Lindb.	r.	
Orthothecium chryseum (Schwaegr.) B. and S.	r.	

LICHENS		
Lecidea lapicida Ach.	f.	Rhizocarpon confervoides DC.
Polyblasia intercedens Lonn.		R. gemmatum
FUNGUS		
An agaric	v.r. (1)	

Although the slope is typically about 20–25° from the horizontal, in places it is steeper and more scree-like, for there are longitudinal patches of stabilised vegetation, chiefly consisting of *Salix arctica*, but with both *S. herbacea* and *Polygonum viviparum* abundant. This suggests zone III or IV (see pp. 387, 388) of a late snow patch, as its position and other considerations prove it to be. The strips of vegetation are a foot to 18 in. (30–45 cm.) broad: the earlier melting of their shallower covering of snow and the steepness of the slope on which they are developed both lead to drier conditions, so that they tend in places to the type described under III (*a*).

(*e*) *Slopes with wet earthy tracts.*

Abundance of cold percolating water from springs or very late melting snow is a frequent feature on slopes both steep and slight. The water renders them almost always dynamic, often locally like a "flowing earth" (**10**), though the most familiar type is that in which long strips[1] of damp barren soil extend down a slight slope and alternate with tracts of larger limestone scree fragments also devoid of plant life.

There may also be ditches with rocky or earthy sides down which most of the drainage takes place. The one investigated drained the remains of a snow patch occupying a cul-de-sac in the hillside, and its barrenness was probably due to the exceptionally late season (end of August even in this good year) in which the snow filling melted. There were no plants at all on its steep earthy banks, but in the trickle of water running down its bed was collected a brown diatomaceous deposit containing *Cymbella arctica* Lagerst., *C. cistula* var. *maculata* (Kütz.) Grun., *C. cymbiformis* var. *parua* W. Sm., *Achnanthes hyperborea* Grun.?, *Fragilaria* sp. and *Schizonema* sp.; while lower down, where the stream bed opened out and was almost dry, the rocks were covered with green algae including *Chaetomorpha* sp. and *Zygnema* sp. There were also patches of *Catoscopium nigritum* Brid. and *Cinclidium arcticum* W. P. Schimper forma, suggesting the beginnings of a moss mat of late melting snow (p. 389) and tending to confirm the supposition that the part above owed its barrenness to the still later disappearance of its snow covering.

(*f*) *Sandy* Dryas *slopes.*

There are no extensive sand beds or dunes on the island, but in one or two places near the coast there are low hills composed of fine limestone sand mixed with larger fragments of the size of gravel. Except where they are relatively well colonised by plants, these hills have steep sides difficult to climb, and the coasts being very windy, the sand is almost continually blown about, especially sweeping up one side to the crest of the hill and then falling down the other, the whole remaining dune-like and dynamic. Few plants can colonise such a habitat, except rhizomatous perennials which grow on limited flatter areas where they can bind the sand. No sand-binding grass is of general occurrence on the island, though Mr Reynold Bray and the expedition meteorologist, Lt.-Com. Langley, reported that there was "a bed of stuff like rye" growing on a sandbank on the west side of the island; a specimen they brought back for identification turned out to be the familiar *Elymus arenarius* L.

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[1] Cf. pp. 359 and 369.

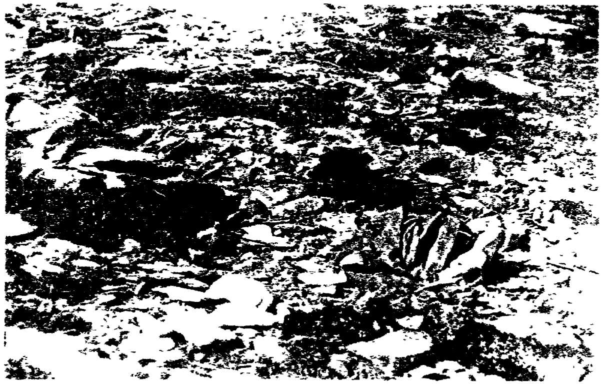
Dryas is generally the chief plant on the sandy hills. In the example listed it grows as flat patches some 10–20 in. in diameter, spaced at variable intervals, but generally covering only a fraction of the surface. Sometimes these patches have the form of longer streaks down the hillside, showing the typical scree nature of such slopes; or with a gentler incline the vegetation may be in horizontal flat *steps* up the hillside, separated by miniature scree slopes of bare sand—a very peculiar formation due to partial stabilisation by vegetation.

The list is short, few of the rather limited equipment of species the island can offer being able to attain ecesis on such dry and dynamic sand:

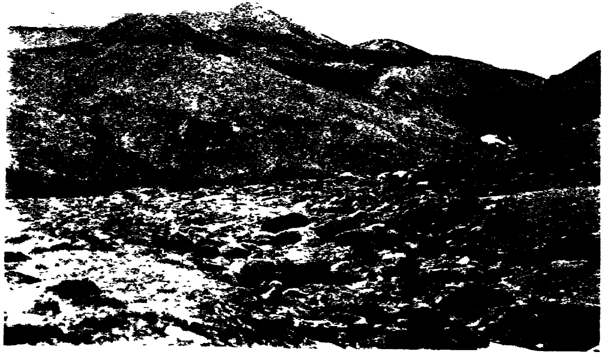
ANGIOSPERMS

Dryas integrifolia Vahl (patches)	a.
Carex nardina Fr. (small tufts binding sand)	f.-a.
Arctostaphylos alpina (L.) Spreng. (patches often large and conspicuously red-blazed)	f.
Epilobium (Chamaenerium) latifolium L. (barren)	o.-l.a.
Saxifraga oppositifolia L.	o.-f.

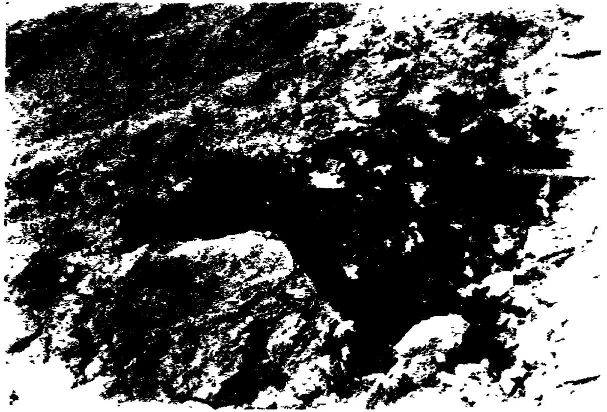
On some slopes with fewer sand particles and more smooth-worn limestone gravel, including many stones 1–3 in. in diameter, the *Dryas* patches are closer together and often support in their centres a conspicuous white patch of *Cetraria nivalis*, while on the larger stones the usual crustaceous lichens occur, chiefly *Lecidea goniophila* Schaer. which may be abundant. On such scree slopes, and indeed sometimes on plateau areas, *Cetraria nivalis*, *C. islandica* and other foliose types of vigorous growth which are not terricolous except on the stablest of earth (and then only as a secondary invasion from the vegetation in which they originally grew), seem frequently to occupy such a position (cf. Pl. XXXIV, phot. 21), growing up and dominating the higher plants which first stabilised the area or at least provided a nidus for the ecesis of the lichens. Since succession involves stabilisation and gradual domination by the biggest plants which can occupy the area, this is not to be considered as a case of retrogression but rather as succession of peculiar type in which a "lower" life form replaces a "higher." The cryptogams here occupy a more advanced position in the sere than the angiosperms on which they grow, and which they dominate and may kill out in these regions of difficult conditions and very severe struggle for existence. They grow as tall as or taller than the angiosperms, are thicker, more luxuriant, and may extend their area farther—probably in relation to their greater tolerance of exposure



Phot. 21. Fjaeldmark on dry valley side: poorly vegetated, frost shattered soil and larger limestone fragments (pp. 374 and 379).



Phot. 22. Bed of watercourse with many dark erratic boulders. Earthy screes in background (pp. 375 and 393).



Phot. 23. The largest plant seen on the island, *Salix arctica* on a rough earthy scree (p. 375). On the right a 1 ft (30 cm.) ruler.

Phot. 24. A ravine inland. The bed is barren but the sides are in places partially stabilised by vegetation (p. 376).

POLUNIN—AKPATOK ISLAND

Face p. 375

when once they have gained a footing. Nor does such lichen colonisation correspond with the well-known rôle of Cladoniaceae on Scandinavian Hochmoors, where species of *Cladonia* and *Cladina* cover the tops of heathy tussocks formed originally by the growth of *Sphagnum*; for this latter invasion follows the death of the dominant ground-shrubs on drying out of the *Sphagnum*, whereas on Akpatok the patches of higher vegetation are hardly raised at all above the surface and in the areas under consideration do not die of their own accord—at least not as a whole.

(*g*) *Dry earthy screes.*

With the soil generally shallow above the limestone rock, and containing many larger fragments, earthy screes are of infrequent occurrence and little importance on the island, except at the foot of some of the more extensive slopes at the sides of creeks such as that behind "Harp Cove." Here we have limited scree-like slopes of fine earthy particles brought down by water and gravity, tight-packed and of clay-like texture, although by August they are baked hard (see Pl. XXXIV, phot. 22, in the background). Running water has worn deep furrows in places and where the sides have caved in, or where the slope is particularly steep, there are irregular or rounded chunks of compacted earth which have broken off and rolled down (see Pl. XXXIV, phot. 23).

The vegetation at best is sparse and open, consisting chiefly of willows and grasses. The latter seem to grow as annuals between the times of movement of the surface (following the melting of the snows) and the drying out of the ground, while the willows are deep-rooted and long-lived, growing best in the more sheltered areas. In fact one specimen of *Salix arctica*, growing on such a rough earthy slope with its deep soil, was about the largest single plant of any kind encountered on the island, though at no point did it reach to more than about 8 in. (20 cm.) above the surface (see Pl. XXXIV, phot. 23).

The following composite list was made from several such areas, the community being generally very sparse, while in places the surface is devoid of vegetation over many square yards. Except where there is a level delta of finely comminuted silty material at the base of the slope, the earth contains larger particles and smooth-worn boulders of limestone. Frequently the willows are in dislodged clumps, with the original roots washed free of soil except at their tips, and adventitious roots growing down from the creeping axes.

ANGIOSPERMS

Salix arctica Pall. (actively colonising delta edges)	f.	Cerastium alpinum L.	r. but constant
S. Hookeriana Barr.?		Trisetum spicatum (L.) Richt.	Absent-r.
Puccinellia angustata (R.Br.) Rand and Redf.	l.a.	Saxifraga aizoides L.	Absent-r.
		Draba lactea Adams (early September second flowering below old axis)	Absent-r.
Polygonum viviparum L.	o.-f.		
Arabis alpina L.	o.-l.f.		
Lychnis apetala L.	o.	Dryas integrifolia Vahl	Absent-r.
Saxifraga oppositifolia L.	o.		

Bryophytes and Thallophytes seem to be absent.

IV. RAVINES.

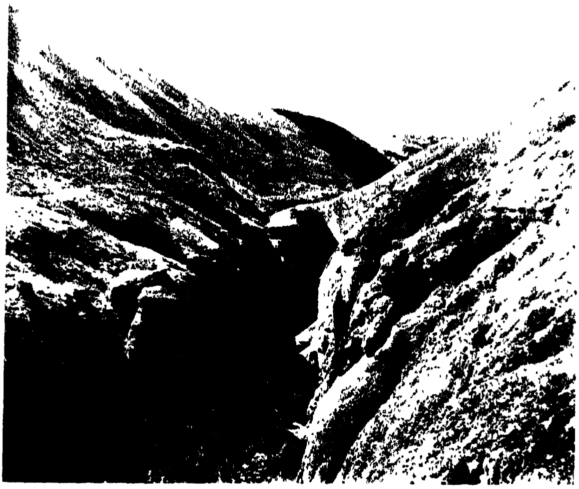
The frequent ravines which make travel so difficult on the island have their origin in small valleys or mere depressions whose water needs an outlet and so starts to cut a little channel (cf. Pl. XXIX, phot. 8). This channel gets deeper and bigger as the valley winds its way towards the sea, where it may cut a way right down through the cliffs to the sea level, and thus have sides 400 ft. or more high, so that the lower part of the valley generally has the form of a narrow canyon bounded by precipitous cliffs.

Whereas the ravines are important physiographically their vegetation is negligible: they are often almost entirely devoid of plant life, and as a whole are so barren that a classification of the habitats they afford would be superfluous. A better idea of their nature and that of the occasional and generally casual plants they support will be gained by tracing the system from inland seawards, aided by a series of photographs.

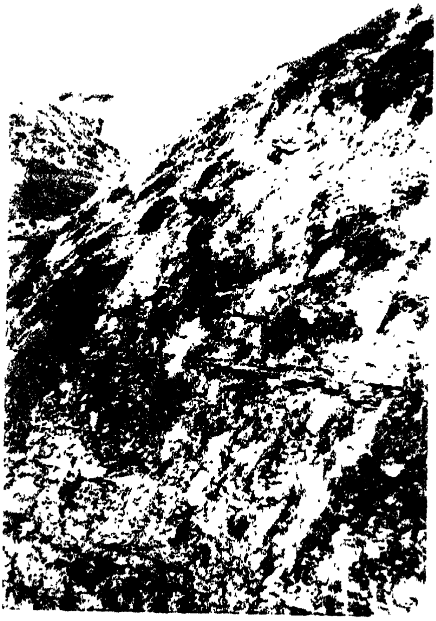
In the interior plateau the "young" ravine is generally like the example shown in Pl. XXXIII, phot. 18. The sides are covered by dynamic and almost barren screes (see III (*b*)). The bed, though certainly containing water at the time of the melting of the snows (when it is probably often a torrent tearing its way seawards), soon becomes completely dry and generally supports no plants at all. Even crustaceous lichens appear to be absent—they take years to grow to an appreciable size and any attempts here would be stopped by water carrying ice, and often rushing so as to grind the limestone fragments against one another, turning them over and about so that the plants are all killed.

Even some miles before the sea is reached, the ravine may have attained the proportions indicated in Pl. XXXIV, phot. 24. Here the sides may be partially stabilised by vegetation, but the bed is largely bare. Even in late summer there is often the remains of a stream trickling along in places, in others disappearing underground. Such a stream may be fairly permanent and support a few filamentous green algae, or it may be quite barren. The rest of the bed is of barren white limestone boulders, although where it is broad and open any raised tracts or spits of sandy beach towards the edge may support anything up to an almost closed community of the usual plateau plants—chiefly Salices, *Dryas* and saxifrages, with mosses of poor growth.

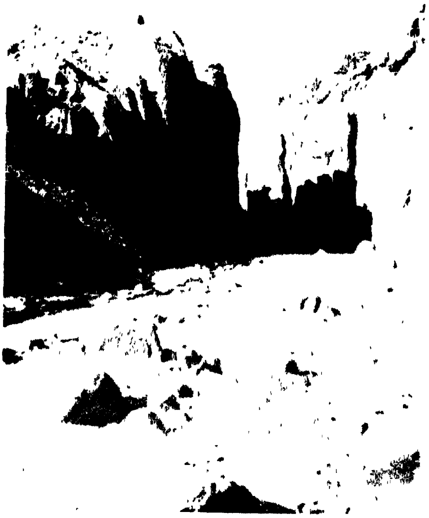
By the time it has reached to within half a mile or so of the sea the ravine is often of the form shown in Pl. XXXII, phot. 15, and Pl. XXXV, phot. 25, tall cliffs forming the sides, frequently with screes above and below. The cliffs are generally barren except where water seeps out of joints and algae can form a slimy investment, but the screes even at the bottom of the cliffs generally support a few of the usual scree plants (see III (*a*)). Pl. XXXV, phot. 26, shows a very well vegetated "old" scree below which even the rounded crumbling top of the cliff supports a number of higher plants, though this is exceptional. The bed often holds water even in September, but these deep



Phot. 25. Older ravine near sea, secondarily cut in valley bed (p. 376).



Phot. 26. Well vegetated scree (above) and crumbling clifftop (below), forming side of old ravine near sea (p. 376).



Phot. 27. Mouth of big ravine near sea. The bed is generally quite barren (p. 377).

ravines are usually so narrow that the whole bed is presumably covered by an almost uniform rush of water in early summer. There is no soil and colonisation by higher plants cannot proceed, while even lichens and mosses rarely attain ecesis except in sheltered crevices on some of the larger boulders.

Pl. XXXV, phot. 27, shows the mouth of a big ravine near the sea. The bed is almost barren, though on the larger boulders a few crustaceous lichens and tiny hard tussocks of moss may occur—especially the yellow *Rhizocarpon geographicum* var. *atrovirens* on the dark erratics which are often a feature among the white limestone, and may sometimes be very numerous (see Pl. XXXIV, phot. 22). Species of *Lecanora* and *Lecidea* may occur in places, while the mosses are generally species of *Hypnum* or *Bryum*, and are for the most part confined to sheltered niches in big boulders—chiefly erratics—though small tufts of *Drepanocladus vernicosus* (Lindb.) Warnst. may occur on cones of sand deposited in their shelter. The only angiosperms are entirely casual—grasses and seedlings of *Polygonum viviparum*, and once or twice a *Salix* bush which had been washed down but managed to attach itself and grow again.

V. VALLEY SIDES.

(*a*) *Damper, better vegetated valley slopes.*

Abundant cold percolating water from springs or melting snow is unfavourable to the development of angiosperms, or indeed of any vegetation, especially when the soil is of the flowing earth type. But where the ground is merely damp at this season (end of August) and the slope is sufficiently sheltered to hold a good and long-lasting covering of snow in winter, we find a comparatively luxuriant vegetation only rivalled on the island by the more lush zones around the lake sides (see p. 381 *et seq.*). These better vegetated valley sides consist generally of tussocky slopes covering some seven-eighths of the area, the rest being occupied by irregular stony depressions 1–3 yards in diameter, and indicative of the original ground-level. The tussocks are of the damper Hillock Tundra type[1] whose formation is alleged to be primarily due to "heaving" of the soil through the action of frost (see Sukachev(**14**)), but which are now covered by a continuous community of mixed ground-shrubs, herbs and cryptogams which have added greatly to their bulk and tussocky form, and so grow on a dark peaty surface soil which is generally very moist. Pl. XXXVI, phot. 28, shows in the foreground an unusually well-vegetated tract, without stony depression or light-coloured lichens, where there is a plentiful supply of fresh percolating water.

The tussocks, and the small furrows of closed vegetation which lie between them, are generally dominated by *Cassiope tetragona* or *Dryas integrifolia*. Often there is a mixed associes of the two, while a marked feature of these damper slopes is the abundance of *Carex misandra*, occasional axes of which may reach 10 in. (25 cm.) in height and be by far the tallest plants of the community; in fact this height is rarely surpassed by any plant on the island. A full list is given below for these areas of closed and comparatively luxuriant vegetation, dominated by angiosperms but with mosses often abundant on the sides of the tussocks or larger raised areas, which they may clothe with rich green tufts. The growth of the lichens, on the other hand, is poor, though everywhere the dark vegetation at the tops of the tussocks is flecked with light patches of *Cetraria nivalis*, varying in size but never more than a few inches across. This, and the flat-topped form of the higher *Cassiope* bushes, indicates that the winter snow covering is even here largely blown away, to form longer-lasting or permanent drifts in any still more sheltered culs-de-sac. Probably the snow lies flat with the tops of the higher tussocks, whose sides are thus well protected from desiccating gales and excessively low temperatures.

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[1] See Part II. The rather similar area described under IX (*e*) in Part II is more limited and specialised, with the hillocks much more pronounced.

Angiosperms

Cassiope tetragona (L.) D.Don.	a.-d.
Dryas integrifolia Vahl	a.-co-d.
Carex misandra R.Br.	f.-a.
Salix reticulata L.	f.
S. arctica Pall.	f.
Saxifraga aizoides L.	f.
Tofieldia borealis (Wahl.) Wahl.	o.-f.
Salix herbacea L.	l.
S. Hookeriana Barr.?	o.
Vaccinium uliginosum var. microphyllum (Lange) Simm.	o.
Polygonum viviparum L.	o.
Saxifraga oppositifolia L.	o.
Pedicularis sp.	o.
Carex membranopacta L. H. Bail.	r.

These species are fairly constant in this habitat; while the six that follow may or may not occur, being generally absent or rare:

Chrysanthemum integrifolium Rich.
Draba sp.
Luzula arctica Blytt
Lychnis apetala L.
Pedicularis lanata Pall. ex Stev.
Pyrola rotundifolia var. pumila Hook.

Bryophytes

Catoscopium nigritum Brid. (pure tufts on edges of wet tussocks)	a.
Bartramia Oldesi Swartz.	
Dicranum groenlandicum Brid.	f.
Hypnum stellatum Schreb.	f.
H. scorpioides L.	f.
Swartzia montana Lindb.	

Lichens

Cetraria nivalis Ach. (small patches)	a.
C. hiascens Th. Fr.	f.
C. islandica Ach.	f.
C. islandica var. tenuifolia (crispa)	f.
Ochrolechia tartarea Massal.	o.
Pertusaria dactylina Nyl.	o.
Alectoria divergens Nyl.	o.
Cladonia pyxidata Hoffm.	r.
Sphaerophorus globosus A. L. Sm.	
S. melanocarpus DC.	

Fungi

Several agarics, a Boletus and a Peziza (?)

The stony depressions.

These, on an average slope, may cover perhaps one-eighth of the area—the depression shown in Pl. XXXVI, phot. 29, is particularly small. They are generally about a foot deep—or rather the tussocks have grown to the height of about a foot from this original ground-level—and have a surface of irregular limestone blocks and stones reposing in a bed of damp soil composed of finely weathered particles of the same rock. Though they may be almost devoid of vegetation (sometimes they approach the "flowing earth" type) and never support more than a sparse open community of herbs and cryptogams, these depressions apparently represent a seral stage only one step lower than the vegetated areas described above. For the large bordering tussocks are extending into their area, chiefly by the tufted growth of such mosses as *Catoscopium nigritum*, while small tussocks are in some places actually arising within them. The following is a composite list from many such areas, some relatively dry, static and well vegetated, others wet and almost barren, or in August consisting of surface-dried, cracking mud:

ANGIOSPERMS			
Saxifraga aizoides L.	f.	Carex membranopacta L. H. Bail.	r.-o.
S. oppositifolia L.	f.	Salix reticulata L.	r.-o.*
Polygonum viviparum L.	Generally f.	Juncus biglumis L.	Absent-o.
Carex misandra R.Br.	o.	Epilobium alpinum L.	Absent-o.
Salix herbacea L.	o.		

* May be absent.

BRYOPHYTES			
Generally absent, apart from the tussocks mentioned			
LICHENS		Polyblasia intercedens Lönn.	
Lecidea sp. or spp. on stones	o.	Cetraria nivalis Ach.	o. fragments
FUNGI		ALGAE	
One agaric	r.	A green filamentous type on wet mud	

(b) *Poorer, dry valley slopes.*

It is often difficult to correlate the difference with any special and observable factor unless it be the absence of a winter snow covering, but where conditions of exposure and available water are not so favourable as those which lead to the type described in the last section a very poor community is developed. Water is not always the obvious master-factor, for some of the poorest slopes may have a perfectly good supply and be quite damp only an inch or two below the surface. The water is, of course, always alkaline or neutral, there being no chance of such a local development of slight acidity as was found towards the tops of some peaty hillocks of hillock tundra, and even of large *Dryas* tussocks elsewhere (p. 371).

In an example selected as typical of these more poorly vegetated valley sides, the angle of slope was slight but the surface was very uneven, there being numerous irregular rocks of varying sizes, and patches of soil interspersed with stones[1]. There are no hillocks or extensive areas of closed vegetation, the photograph (Pl. XXXIV, phot. 21; also cf. Pl. XXXIII, phot. 19) showing how the plants are generally limited to little irregular patches, or lengthened tracts a few inches wide which in places show something like the polygons described in Section II (*a*), for the deposition of the larger rocky fragments roughly along these lines is rather suggestive of this type of ground, so much better seen on the exposed plateau above. These poor and dry valley slopes constitute a less extreme facies with better vegetation than generally occurs on the plateau, as is seen from the frequencies given in the following list.

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[1] This is a fjaeldmark, or stony desert. Also cf. Ramann's "Detrital soils of cold regions" (**10**).

The vegetation only covers about one-sixth to one-eighth of the area. As on the plateau polygons, the most important plant is *Dryas integrifolia,* and its hard, close tufts growing 1–2 in. in height form the core of almost all the patches and strips of vegetation, which show up dark against the strikingly light-coloured background of frost-shattered limestone. The most abundant associated plant is *Saxifraga oppositifolia,* chiefly growing in the sides of the *Dryas* tufts.

Evidently the slopes are blown almost bare of snow in winter, for light-coloured patches of *Cetraria nivalis* often relieve the dark *Dryas* tussocks on which they grow, while growth is much better in the lee of the larger rocks, where lichens, particularly *Cetraria* spp. and *Alectoria divergens,* mixed with *Dryas,* often form a thick mat. Elsewhere the lichens, though abundant and including numerous species, are of poor growth, the rocks being almost bare, even of crustaceous types, while the mosses are few.

ANGIOSPERMS			
Dryas integrifolia Vahl	a.-d.	C. membranopacta L. H. Bail.	o.
Saxifraga oppositifolia L.	a.	Salix reticulata L.	o.
Cassiope tetragona (L.) D Don	f.	Draba Bellii potius ad oblongatum	r.
Saxifraga aizoides L.	f.		
Salix arctica Pall. (agg. ?)	f.	Silene acaulis L. (tussocks)	r.
Carex misandra R.Br.	f.	Carex scorpioides Michx.	Absent-r.
Polygonum viviparum L.	o.-f.	Juncus albescens (Lange) Fernald	Absent-r.
Salix arctica Pall. (dwarf form)	o.		
Carex nardina Fr.	o.	Pedicularis lanata Pall. ex Stev.	Absent-r.
BRYOPHYTES			
Grimmia sp.?	o.	Bryum sp.?	o.
LICHENS		C. islandica var. tenuifolia (the biggest tussock in Pl. XXXIV, phot. 21, is largely covered by it)	o.
Alectoria divergens Nyl.	l.a.		
Cetraria nivalis Ach.*	l.a.		
Lecanora verrucosa Laur.	f.	Ochrolechia tartarea Massal.	o.
Lecidea lithophila Ach.	o.	Lecanora epibryon Ach.	o.
L. goniophila Schaer.	o.	Rinodina roscida Lynge	o.
L. lapicida Ach.	o.	Cladonia pyxidata Hoffm.	r.
L. Berengeriana Nyl.	o.	Caloplaca ferruginea Th. Fr.	
Cetraria cucullata Ach.	o.	Protoblastenia calva A. Zahlbr.	

* Bottom right-hand corner of Pl. XXXIV, phot. 21—indicates absence of snow covering.

FUNGI	CYANOPHYCEAE
Ustilago caricis on fruits of *Carex misandra*	Under damp stones

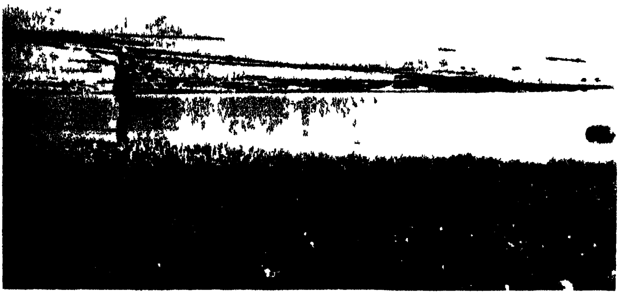
(*c*) *Grassy valley sides.*

Some of the most sheltered valley sides which have a well-drained sandy soil as opposed to a frost-shattered limestone surface are largely dominated by grasses. Occasionally patches are quite meadow-like in their luxuriance (cf. IX (*a*) 2 in Part II). Again, as exposure and water conditions change, they show all stages of transition to the ordinary types of valley side described above (Section V (*a*) and (*b*)). In some cases the grassy patches seem to owe their maintenance in part at least to the action of polar bears, for the willows colonising them are uprooted and there are turfy sods strewn about.

The best example of this grassy vegetation is described later as a "special localised community."

Phot. 28. Damp unusually well vegetated tract in sheltered valley (p. 377).

Phot. 29. Relatively luxuriant and healthy (but not quite continuous) vegetation on damp and sheltered area near bottom of valley.



Phot. 30. Small shallow lake on exposed plateau. One side is largely barren, the other vegetated by a closed community of cotton grasses (p. 381).

VI. VALLEY HEADS AND DEPRESSIONS.

In the heads of valleys and the deeper and more sheltered depressions with no outlet for their water the best bogs on the island are to be found, though they vary with water conditions. Sometimes they are no more than damper facies of the "marshy areas" described under IX (*d*) Part II, but in other cases even where there is no permanent body of standing water they may be deep and stagnant, though rarely acidic in reaction. Where there is a permanent lake its sides generally support zones beginning with a lush bog nearest the water, in contrast with the usual lakes in exposed situations on the plateau, whose margins may in places be almost barren (see Pl. XXX, phot. 11).

(*a*) *Lake marginal zonation.*

Several of the photographs (Pl. XXX, phot. 11, Pl. XXXVI, phot. 30) show how variable may be the marginal vegetation of lakes and pools, especially on the exposed plateau. Thus a small lake may have one side almost entirely barren and the other vegetated by a closed community of *Eriophorum* in the manner shown in Pl. XXXVI, phot. 30. It seems that where the dissimilarity is so well marked, the side from which the prevailing gales come (north-west) is most often the better vegetated, the other side, to the south and south-east, being liable to violent lashing by quick wavelets driven hard by these gales, which are very frequent. It is thus too disturbed to become well vegetated, and where colonised generally develops a definite line dividing the lake from the boggy margin, in contrast with the other side which may have Eriophora or *Pleuropogon Sabinei* growing out and colonising the open water near the edge.

In these exposed and disturbed situations the marginal zonation is little marked, though there may be a drier region of *Carex membranopacta* L. H. Bail. behind the waterside plants, before the ordinary plateau is reached. Any region dominated by Eriophora occurring here is hardly a bog, the humus being shallow and the community often interrupted by projecting limestone boulders or tracts of drier hillock tundra.

The few lakes occurring in sheltered situations are bounded, where the margin is flat, by luxuriant bog-vegetation into whose wet humus the feet may sink for as much as a foot. An especially luxuriant example in a valley towards the south end of the island showed the following zonal sequence:

(1) *Eriophorum polystachion* L. growing out into the water. It was thick near the margin where the bed was of mud and the water only a few inches deep, but got thinner beyond till it stopped where the depth exceeded a foot.

(2) *Eriophorum polystachion* and *Carex membranopacta* in an almost closed mixed "reed swamp" community growing in the shallow water at the margin, with the latter more dominant where the community extended out of the water and formed a slight bank. From this grew a few large conspicuous leaves of *Petasites sagittatus* (Pursh.) A. Gray, found nowhere else on the island.

(3) The real bog (or "fen", since it is neutral in reaction, the lake being supplied by a stream of spring water) is formed by mosses of tufted growth, into whose wet surface the feet may sink 8 in. or more. The chief moss is *Aulacomnium papillosum* Jaeg., and growing among the mosses are the following vascular plants:

Carex membranopacta L. H. Bail.
C. rariflora (Wahl.) Sm.
Deschampsia alpina (L.) Roem. and Schult.
Equisetum variegatum Schl.
Eriophorum polystachion L.
Pedicularis sp. or spp.
Petasites sagittatus (Pursh.) A. Gray
Poa alpina L.
P. rigens Hartm.
Polygonum viviparum L.
Salix Hookeriana Barr.?

The mosses were too deep and luxuriant for small bog plants, though in places the more hygrophytic species in the above list (especially the *Eriophorum*) formed an almost closed community above the moss layer. The grasses were chiefly in drier places near the margin, but the *Salix* was almost everywhere in evidence, with its silvery, hairy leaves on axes rising just 4 in. above the surface before being killed by winter. It is suggested that this height may indicate the depth of winter snow in sheltered situations, and if this is correct the fall would thus be no more than a very few inches.

(4) Away from the water supply, where the level began to rise to the valley slopes, the grasses became largely dominant, and soon passed into the community described under IX (*a*) 2 in Part II. In less favourable situations the bog passed instead into a polygon or fjaeldmark area of *Dryas*, *Salix arctica*, etc.

The peculiar hummocks of humous material described in Part II under XI (*a*) 3 ("permanent lakes") as rising from the shallow beds of one series of lakes in a large but sheltered valley in the north of the island, are in some cases (towards the margin of the lake) several yards in diameter, with their centres raised, less boggy, and sometimes hard and dry. Certain of the species in the following considerable list composing the mixed grassy vegetation on these larger hummocks again suggest an increased nitrate supply (cf. lists from the tops of bird-cliffs, Part II) due to the flocks of small waders inhabiting the locality and perhaps to visits of larger birds on migration.

Arctagrostis latifolia (R.Br.) Griseb.
Carex membranopacta L. H. Bail.
Chrysosplenium alternifolium L.
Cochlearia fenestrata R.Br. (robust growth)
Deschampsia alpina (L.) Roem. and Schult.
Equisetum arvense L.
E. variegatum Schl.
Eriophorum polystachion L.
E. Scheuchzeri Hoppe
Festuca rubra var. arenaria (Osb.) Fr.
Juncus biglumis L.
Phippsia algida (Soland.) R.Br.
Pleuropogon Sabinei R.Br.
Poa rigens Hartm.
Ranunculus hyperboreus Rottb.
Salix arctica Pall.
Saxifraga caespitosa L.
S. rivularis L.
Stellaria longipes Goldie

(*b*) *Boggy dips without lake.*

Depressions which have no permanent lake but are nevertheless drained very slowly, if at all, may support small but luxuriant bogs if they are sufficiently sheltered. On the other hand they must not be so filled with snow in winter that their growing season is greatly reduced by its late melting. The poorer facies on the plateau are described under IX (*d*) (Part II); these deeper bogs sometimes develop a slight acidity and are similarly marked by overwhelming dominance of one species, often to the complete exclusion of others, for the area is relatively favourable for vegetation, with its shelter and snow covering, and an aggressive species can cover it alone. The chief plants playing this part are *Eriophorum Scheuchzeri*, *E. polystachion*, *Carex membranopacta* and several of the more hygrophytic grasses, especially *Arctagrostis latifolia*. But where the area dries out towards the end of the growing season the surface may be made irregular by hillocks, and this irregularity of habitat is liable to break the continuity of the dominant species.

VII. SNOW EFFECT.

Under this heading will be considered not the obvious ameliorating effect of a slight winter snow covering[1] on the vegetation of the limestone plateau, but such more specialised areas as are in one way or another greatly modified by having each winter a thick drift of snow accumulating about them.

(*a*) *Swallow holes*.

These are the "swallow holes" through which water drains in early summer in the many valleys and smaller depressions of the plateau from which there is no outlet by ordinary surface drainage. Larger valleys may have a number of these swallow holes close together at their bottoms; small depressions may have only one or two, but always the holes have the form of funnels which are rarely more than 5 ft. deep or 15 ft. broad. They must be filled with snow in winter, and if they lie in a small deep depression this holds a larger drift, as is indicated by a certain amount of "late snow patch" zonation (see VII (*b*) below) round its sides. Nearer the centre such a snow-holding dip generally has the appearance of the drying bed of a temporary lake, as in a sense it is, and even at the end of August may be muddy and almost barren, like the centre of the swallow hole itself.

This type may for the present purpose be called the "late snow run-off" swallow hole, in contrast with the "early snow run-off," where the sides of the hole are clothed with a luxuriant tangle of *Taraxacum* and *Oxyria* (see below). The late type only becomes bare of its snow or water towards the end of the growing season, and its vegetation at best is an open community of ephemerals whose growing season is further shortened by the dynamic and otherwise inhospitable nature of the slowly draining and drying surface.

The hole investigated in the late snow run-off area was about 10 ft. broad at the top and 4 ft. deep, and as it drained the whole of an area of many hundreds of square yards it must have carried in summer a fairly fast and permanent flow of water, though whether this took the form of a visible gush or a mere imperceptible trickle down the sides could not be ascertained from an examination of the dried condition. The hole was an almost perfectly formed funnel, narrowing below to a small patch of limestone mud filling the bottom. The surface of this mud was dry and cracking in early September, but it was nevertheless able to support a few tiny seedlings of *Cardamine pratensis* L. and several small vegetative tufts of the moss *Ceratodon purpureus* Brid. forma.

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[1] Cf. the very effective damping down, under the snow, of atmospheric temperature fluctuations noted by Helland-Hansen (**22**) and Polunin (**23**).

The steeply sloping sides of the hole were also of fine silty particles closely packed and generally barren, while the appearance at the top of occasional bare waterworn stones showed that at least part of the water gushed over in times of quick melting, or when the outlet below was suddenly cleared by the melting of ground ice. Below, the surface of the main depression sloped slightly towards the hole in the centre. Near the hole its sides were muddy, with barren dark brown tracts of pebbles embedded in wet mud. But in places these were covered by what was so nearly a mat of *Pleuropogon Sabinei* R.Br. as to suggest that during part of the growing season the area is a lake, while in drier parts *Deschampsia alpina* (L.) Roem. and Schult. was frequent, and locally formed almost closed colonies, with occasional non-flowering plants of *Cardamine pratensis* L. *Hypnum scorpioides* L. was the chief moss. It formed especially large tussocks at the sides of a little trickle of water, in which were abundant diatoms and *Zygnema* sp., and about which also grew *Cardamine pratensis*, *Equisetum variegatum* Schl. and much *Ranunculus hyperboreus* Rottb.

It thus seems that during part of the growing season the area is a lake of fairly constant depth and surface level; the water coming from the melting of the surface snow being prevented from running away by the blocking of the run-off hole by ice. It is then that the typical lakeside *Pleuropogon* develops, following down the damper tracts as the water leaves them and flows away when the hole begins to function. The *Deschampsia* probably develops later, when the surface has dried out, from propagules which have survived the winter, playing the part of an annual colonist with a hazardous life.

Nearer the margin of the depression the snow is probably shallower and thus clear for colonisation earlier in the summer. *Pleuropogon Sabinei* persists in some of the damper places though it is of poor growth and does not flower, but the chief community consists of tussocks of *Deschampsia alpina* of the type mentioned under XI (*a*) (Part II).

The "early snow run-off" holes are much drier in August and seem individually to drain a much smaller area, or a small snow patch which melts so quickly that the surface around dries out at an early date. Generally the zones of this snow patch follow the sequence indicated in VII (*b*) below, with *Salix herbacea* especially abundant, while the sides of the hole itself typically consist of soil containing coarse sand particles which promote good aeration. The vegetation of these sides is remarkable—a luxuriant tangle of *Taraxacum* sp. and *Oxyria digyna*, both typically growing better than in any other situation. With these are almost always associated clans of *Veronica alpina* L. and *Potentilla alpestris* Hall forma, and sometimes one or more of the grasses of well-drained and aerated soils. Almost exactly similar examples were frequently encountered in the west-central plateau and near the south point of the island, though *between* these regions hardly a plant of the *Veronica*, the *Potentilla* or even the *Taraxacum* was seen. This peculiar association was at first thought to have some relation to the "earths" of the Arctic foxes, the entrances to which were sometimes found at the bottom of the snow holes, but in other cases no signs of foxes could be discovered. A remarkable snow-hole in the valley of lush vegetation near the south point of the island was no broader than usual at the top, and had its sides covered by the same luxuriant tangle, with the following composition:

Oxyria digyna (L.) Hill	co-d.	Salix herbacea L.	f.
Taraxacum sp.	co-d.	Poa alpina L.	f.
Veronica alpina L.	a.	Salix reticulata L.	o.
Potentilla alpestris Hall forma	l.a.	Astragalus alpinus L.	o.

There was a gully cut in the side at one point, and at its base abundant *Polygonum viviparum* and grasses. These well-vegetated sides extended to a depth of about 5 ft., but instead of a sandy or muddy bottom there was a deep hole with sides of broken limestone rock, in places almost perpendicular, dripping wet, and with a saturated atmosphere. Rooting in the joints of these sides grew the following:

Cystopteris Filix-fragilis (L.) Chiov. v.a.
Ranunculus affinis R.Br.
R. hyperboreus Rottb.
Chrysosplenium alternifolium L.
Saxifraga caespitosa L.
Poa alpina L.
Festuca rubra var. arenaria (Osb.) Fr.

BRYOPHYTES
Camptothecium nitens Schp.
Hypnum stellatum Schreb.
Mnium hymenophyllum B. and S.
Philonotis fontana var. adpressa (Ferg.) Limpr.

These mosses grew particularly well near the bottom, which lay at a depth of about 12 ft. below the general ground-level and was of barren wet sand, with pools of seepage water. On the sides near the bottom were a few vascular plants, all markedly etiolated, of a light colour, and with long drawn-out limp shoots:

Saxifraga cernua L.
S. caespitosa L.
Arabis alpina L.
Oxyria digyna (L.) Hill
Cystopteris Filix-fragilis (L.) Chiov.

(*b*) *Late snow patches.*

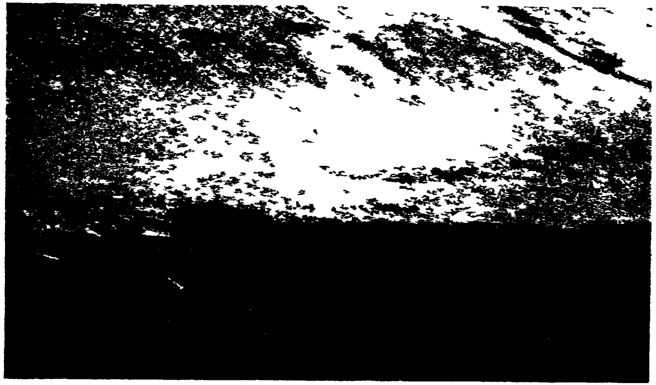
While the occasional patches of snow still existent on the island in late summer are in deep ravines and rocky dips with little vegetation (for their snow is probably permanent), there are many more exposed spots behind ridges and in slight depressions, which give every indication of having a good snow covering lasting well into the growing season. Such "late snow patches" are recognised by the typical "late snow plants" (15) which inhabit their inner zones, while the surrounding area has little or no snow covering and consequently supports a different and generally much poorer vegetation.

The vegetation of these late snow patches is so typical and on the whole so constant in its component species, that a single example was selected for more intensive examination and photography. It had a wide ledge running back some 30 yards into the side of a broad ravine, whose banks rose steeply above. The patch, part of which is shown in Pl. XXXVII, phot. 31, was about 50 yards long and bore vegetation exactly similar to that of a sheltered dip on the less exposed plateau, although such dips generally show a less perfect zonation. The ledge evidently collected a deep "drift" of compacted snow which melted very slowly in the summer. Everything must be well covered and protected in winter, and even when the outer zones are exposed in early summer there is for a long time a continuous supply of melting snow water from the snow still covering the central parts, which are not exposed until much later. The zonation is well marked, especially towards the outside, where the vegetation is relatively luxuriant.

(I) The outermost zone begins near the edge of the ledge and extends inwards for about 4 yards. It is characterised by the dominance of *Dryas* rather than *Cassiope*, and by the abundance of *Cetraria nivalis*, which is absent from all other parts of the late snow patch, and indicates that this outermost zone has a poor or negligible snow covering in winter. Other lichens are much in evidence, and also *Carex misandra*, whose leaves make the part photographed (Pl. XXXVII, phot. 32) look almost grassy. The area gave the following list:

ANGIOSPERMS			
Dryas integrifolia Vahl	a.-d.	Draba sp.	r.
Cassiope tetragona (L.) D.Don.	a.	Polygonum viviparum L.	r.
Carex minandra R.Br.	l.a.	Puccinellia angustata (R.Br.) Rand and Redf.	r.
Vaccinium uliginosum var. microphyllum (Lange) Simm.	f.	Carex nardina Fr.	r.
Salix arctica Pall.	f.	C. rupestris All.	r.
S. reticulata L.	f.	Rhododendron lapponicum (L.) Wahl.	r.
Silene acaulis L.	o.		
Saxifraga oppositifolia L.	o.		
BRYOPHYTES			
Tetraplodon mnioides B. and S.		Hypnum sp.	
		Drepanocladus sp.	
LICHENS			
Cetraria nivalis Ach.	v.a.	Ochrolechia tartarea var. frigida	f.
Lecidea Berengeriana Nyl.	v.a.	Pertusaria dactylina Nyl.	f.
Sphaerophorus globosus A. L. Smith	a.	Cladonia mitis Sandst.	f.
Ochrolechia tartarea Massal.	f.	Cetraria cucullata Ach.	o.
Cetraria islandica var. tenuifolia Wain.	f.-a.	Alectoria divergens Nyl.	o.

(II) This is the broad zone with *Cassiope tetragona* overwhelmingly dominant as is shown in Pl. XXXVII, phot. 33. It is a typical "ground-shrub mat" (**16**) with associated herbs and cryptogams, but in places towards its inner limit, where the ground is damper, it may have a less regular surface with small hillocks. These have vegetation evenly distributed over their tops and sides, and thus show no indication of the microclimates exhibited on other such



Phot. 31. Looking across the late snow area described in the text. Most of the zones are just distinguishable (pp. 386, 38[illegible]).

Phot. 32. Outermost zone (I) of late snow patch. *Dryas* with much *Carex misandra*, also white *Cetraria nivalis*, indicating a relatively poor winter covering (p. 386). Ruler measures 1 ft.

Phot. 33. *Cassiope* heath zone II in late snow area. The mat includes some *Salix reticulata* (rounded leaves) and *Dryas* tussock in fruit in upper right hand corner, coin size of English penny (p. 386).

POLUNIN—AKPATOK ISLAND

Face p. 387

hillocky areas with a less thick and lasting snow covering. This is to be expected if we remember that these particular hillocks are protected by a snowdrift until well into the growing season.

Besides the better snow covering, this *Cassiope* zone also differs from the outer, poorer *Dryas* zone (I) in its *p*H values. Except on its extreme outer edge, which was of the usual frost-shattered soil of limestone origin, zone I had mixed with its surface humus many gritty particles of silica apparently deposited by some geodynamic processes, and amongst them, just under the surface, the soil was slightly on the acid side of neutrality, about *p*H 6·5. In the *Cassiope* zone the surface soil was a loose and doubtless well-leached sand containing much brown humus, and very distinctly acid (*p*H 5·5–6·0), being almost of the heath type to which its vegetation conformed.

ANGIOSPERMS			
Cassiope tetragona (L.) D.Don.	d.	Saxifraga oppositifolia L.	o.
Dryas integrifolia Vahl	a.	Polygonum viviparum L.	o.
Vaccinium uliginosum var. microphyllum (Lange) Simm.	f.-a.	Poa rigens Hartm.	o.
		Luzula arctica Blytt	o.
Carex misandra R.Br.	a.	Carex membranopacta L. H. Bail.	o.
Salix reticulata L.	f.	Pyrola rotundifolia var. pumila Hook.	r.
Empetrum sp.	o.		
Arctostaphylos alpina (L.) Spreng.	o.	Pedicularis sp.	r.
Salix arctica Pall.	o.	Tofieldia borealis (Wahl.) Wahl.	r.
BRYOPHYTES			
?	a.	Camptothecium lutescens B. and S.	f.
Meesea trichodes Spruce	a.	Trichostomum tortuosum Dixon	f.
LICHENS			
Ochrolechia tartarea Massal. var. frigida	a.	Peltigera venosa Hoffm.	f.
		Cladonia pyxidata Hoffm. var. pocillum Wain. (and probably some of type)	f.
Cetraria islandica Ach. var. tenuifolia (crispa) (tufts up to a foot across)	a.		
		Cetraria nivalis (towards outer margin of zone)	r.
C. hiascens Th. Fr.	f.		

(III) The third zone is often not so well marked as the others, especially in the late snow patches where snow lasts longest. It consists of a belt marked by the abundance and frequent dominance of dwarf willows, particularly *Salix reticulata*, though the community is no longer closed, and doubtless represents a lower stage in the seral tendencies than the dwarf-shrub mat outside, from which it constitutes a transition to IV (see below). The *p*H value is but doubtfully on the acid side of neutrality. More interesting is the first definite appearance of true late snow types, for the *Cassiope* zone is merely one of good winter snow covering and not of particularly late melting.

Salix herbacea is the most conspicuous of the late snow contingent, and when it is as abundant and luxuriant as in this zone, an infallible indicator of late snow both in Greenland (**15**) and Northern Lapland (**17**). *Oxyria digyna* is another good late snow indicator here, since it is an open soil plant.

ANGIOSPERMS			
Salix reticulata L.	a.-d.	Tofieldia borealis (Wahl.) Wahl.	f.
S. arctica Pall.	a.	Saxifraga oppositifolia L.	o.
S. herbacea L.	l.a.	Carex bipartita All.	r.
Luzula arctica Blytt	f.	C. scirpoidea Michx.	r.
Saxifraga aizoides L.	f.	Oxyria digyna (L.) Hill	r.
Polygonum viviparum L.	f.		

Cryptogams are not much in evidence, though most of the species given in the list for zone II also occur here, further emphasising the poor definition of this *Salix* zone (III). The surface centimetre of soil is dark brown and humous, although the community is incompletely closed. Pl. XXXVIII, phot. 34, shows a better marked example of this zone from another late snow area. It has pure dwarfed *Salix reticulata* interrupted only by pieces of limestone.

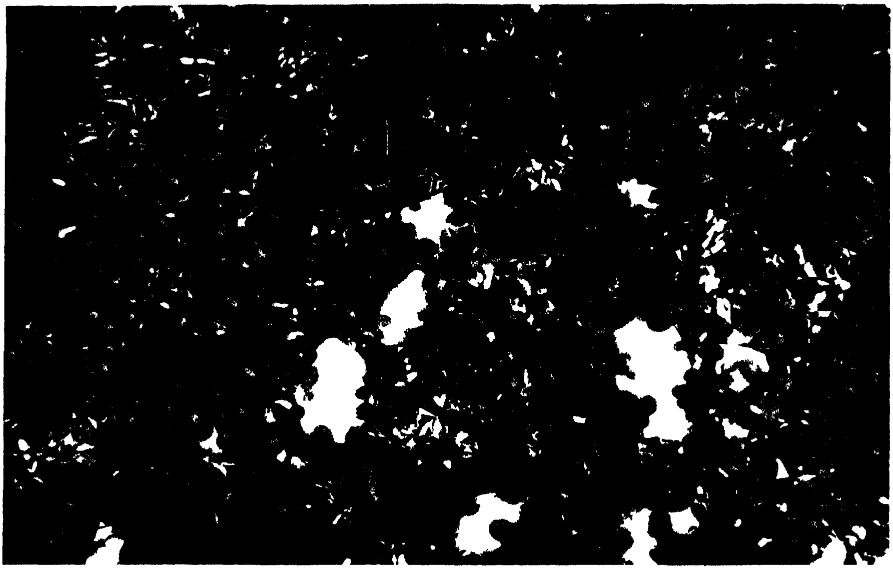
(IV) This follows directly inside III and is a fairly broad zone clearly marked by the dominance of *Salix herbacea* and the abundance of *Polygonum viviparum* (see Pl. XXXVIII, phot. 35). The ground is dark and rendered uneven by cracking and the growth of tiny plants, which also make the surface loose in texture. By this dark colour of the *Salix herbacea* zone, which is often quite extensive, the late snow patches can be recognised from afar in this light-coloured limestone country. On closer inspection the darkness of the *Salix herbacea* zone is seen to be relieved by small grey patches of lichens, chiefly *Lecidea petrosa*. The ground is wet under the surface almost throughout the (greatly shortened) growing season, as is indicated by the typical late snow flora, though the surface humus, which is approximately neutral, appears quite dry.

ANGIOSPERMS			
Salix herbacea L.	d.	Oxyria digyna (L.) Hill	o.
Polygonum viviparum L.	a.-co-d.	Draba oblongata forma ad Bellii	o.
Salix arctica Pall.	f.	D. alpina forma	
Carex bipartita All.	f.	Carex misandra R.Br.	
Lychnis apetala L.	f.	Chrysanthemum integrifolium Rich.	r.
Cerastium alpinum L.	f.	Alsine Rossii (R.Br.) Fenzl	r.
Poa alpina L.	o.	Saxifraga aizoides L.	r.
Trisetum spicatum (L.) Richt.	o.		
Saxifraga oppositifolia L.	o.		
BRYOPHYTES		Drepanocladus uncinatus (Hedw.) Warnst.	o.
Bryum sp. (barren) near nitidulum	o.	Sauteria alpina N. and E.	
LICHENS			
Lecidea petrosa	a.	Placynthium asperellum Trev.	o.*
Cladonia pyxidata var. pocillum	o.	Protoblastenia calva	
FUNGUS			
An agaric	o.		

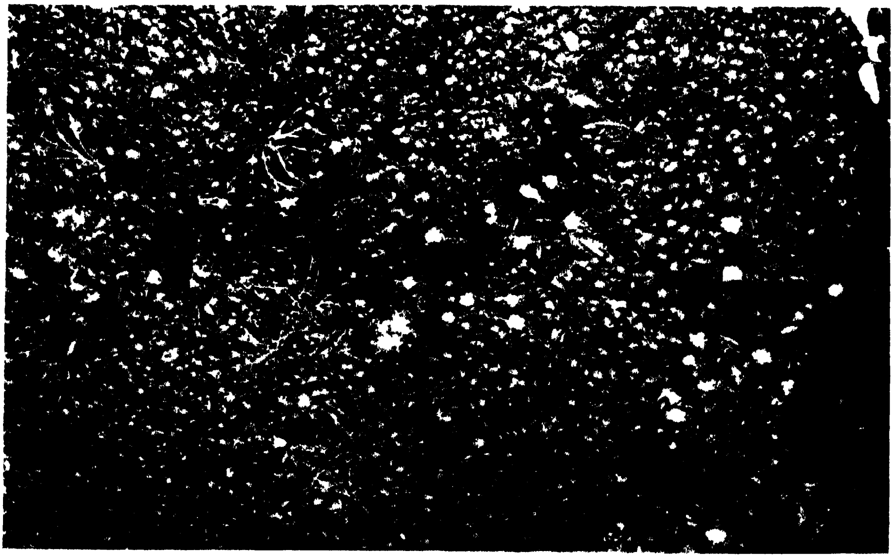
* On loose splinters of limestone.

(V) Inside the *Salix herbacea* zone comes a belt not always so well seen in other examples—a belt of light-coloured soil almost devoid of vegetation, or at best supporting no more than an ephemeral community. For it is here, towards the back of the ledge, that the snow lasts longest, and the ground is waterlogged for a long time after it is gone—in a wet season perhaps till winter comes again. The area usually consists of irregular blocks of limestone and smaller fragments set in a fine-grained soil, which when its surface dries out becomes hard like the centre of a polygon.

The soil water tends to the alkaline side of neutrality and the community at best is a sparse open one, though the number of colonists may be considerable, as Pl. XXXIII, phot. 20, and the following list show:



Phot. 34. *Salix reticulata* looking down on pure society in zone III of late snow patch (pp. 387, 388). The white patches are pieces of uncolonised limestone.



Phot. 35. Looking down on *Salix herbacea* (tiny round leaves) with abundant *Polygonum viviparum* (white flowers) forming zone IV of late snow area (p. 388).

POLUNIN—AKPATOK ISLAND

ANGIOSPERMS

Oxyria digyna (L.) Hill	f.-a.	Braya purpurescens (R.Br.) Bunge	(I)
Saxifraga oppositifolia L.	f.	Alsine Rossii (R.Br.) Fenzl	(I)
S. cernua L.	f.	Arabis alpina L.	(I)
S. caespitosa L.	f.	Draba fladnizensis × micropetala (D. glabella Pursh.)	(I)
Cerastium alpinum L.	o.		
Phippsia algida (Soland.) R.Br.	o.	D. lactea Adams vel fladnizensis Walp. × lactea	(I)
Salix arctica Pall. (dwarf form)	r.		
Trisetum spicatum (L.) Richt.	r.	Single specimens of two other Drabae	

BRYOPHYTES

Hypnum stellatum Schreb.

Fimbriaria sp.

Sauteria alpina N. and E.

LICHENS: mostly crustaceous forms on any blocks or large splinters of limestone:

Placynthium asperellum Trev.	f.	(on loose stones)
Protoblastenia calva A. Zahlbr.	f.	
Lecidea spp.		

(VI) Just in the angle of the dip, where the snow lasts longest of all and leaves a small deposit of dried mud from the collected dust falling annually on the surface and making old patches of snow quite dirty, is another dark patch a few yards long. This time it is an almost pure family of *Grimmia apocarpa* Hedw., and within its limited area (see Pl. XXXVII, middle background in phot. 31) the following angiosperms occur:

Saxifraga cernua L.	f. (several)	Arabis alpina L.	(I)
Phippsia algida (Soland.) R.Br.	(I)	Poa alpina L.	(I)

It is interesting to note that mosses on the whole increase towards the centre of the late snow area, water being more abundant and competition almost absent. On the other hand lichens decrease markedly and may be absent from the centre, the growing season being too short for them where the snow melts so very late.

Above zone VI comes a slope of limestone shale with at first, towards the bottom, practically no vegetation, except occasional dead axes of *Saxifraga cernua*; above is a *Salix herbacea* zone much poorer and narrower than the one on the ledge below, with a still poorer subsidiary flora. This is the greyish band on the slope near the top of Pl. XXXVII, phot. 31—its soil is much less dark and humous, for the slope is now very dry and must drain out comparatively soon after the melting snow has left it exposed. Then comes a narrow, more stable zone of larger Salices which shows as a darker upper margin to the last zone; and after that the bare face of a limestone cliff. Thus within the bounds of edaphically limited possibilities the zonation of vegetation under the retreating snow patch is repeated up the side of the ravine where this is covered in winter.

(c) *Persistent snow patches.*

In sheltered places in deep ravines and valleys there are patches of compacted snow or ice still left on the island at the end of August. Though their surface may melt fast in the sunshine, some at least are permanent and show more or less perfect zonation from the barren ground near the compacted snow to the relatively well-vegetated "late snow" areas farther out. The patch investigated was still about 400 yards long at the time and is seen on the right-hand side of Pl. XXXIX, phot. 36. The ground all round it is barren, for it has cleared of its covering too late in the season for anything to grow. There is not even a moss mat in the run-off directly below, though where the ice-cold water drips off the edge of the snow to form a little muddy pool are stones with an investment of *Phormidium* sp.

Some yards below the thick, slowly retreating edge of the snow, on the damp mud and shingle slopes seen in the photograph, are to be found the first angiosperm colonists—occasional little specimens of *Saxifraga cernua* L. and *Phippsia algida* (Soland.) R.Br., which seem to be followed by *Puccinellia angustata* (R.Br.) Rand and Redf. and a dwarf form of *Salix arctica* Pall. On the mud and stones hereabouts are small tufts of *Bryum* sp. and *Webera albicans* Schp.

Lower down, and still farther away from the snow, green tussocks of *Webera albicans* clothe the banks of the little streams of snow water, in which are communities of filamentous algae dominated by *Zygnema* but with much *Spirogyra* and *Oscillatoria* also. Beyond these banks are mossy areas with the *Webera* generally dominant but intermixed with much *Bryum* spp. (including *B. pseudotriquetrum*), and with *Drepanocladus vernicosus* (Lindb.) Warnst. In the drier places the growth of the mosses may be tussocky, the vegetation being incompletely closed, and here grow a considerable number of more or less hygrophilous angiosperms:

Saxifraga caespitosa L.
S. cernua L.
S. oppositifolia L.
Salix vestita Pursh.
Drabae
Cerastium alpinum L.
Lychnis apetala L.
Poa alpina L.
Deschampsia alpina (L.) Roem. and Schult.
Puccinellia angustata (R.Br.) Rand and Redf.
Trisetum spicatum (L.) Richt.
Carex membranopacta L. H. Bail.
C. bipartita All.
Equisetum arvense L.

In spite of the number of species with the grass habit that occur, the area does not appear any more grassy than the rather similar one listed on p. 389, for most of the angiosperms are no more than occasional, and grow chiefly at the lower end of the mossy zone, the end away from the snow patch. They seem to belong to zone V (cf. p. 388) of a persistent snow patch whose surrounding areas, especially below, are kept wet and hence mossy by the melting snow. The almost pure mosses above, representing zone VI (cf. p. 389), are wet, and persist down the moist sides of the streamlet. It is only towards the bottom of the rising slope on the other side of the stream (left-hand side of Pl. XXXIX, phot. 36) that the earlier cleared *Salix herbacea* and other zones are found, thus indicating the very much greater extent of the snow drift earlier in the growing season.

As is frequently the case, there is below this snow patch a small but deep pool fed by the stream of snow water described above. The level of the water in this pool is kept constant by an overflow stream going down the valley, and so it is relatively well vegetated, with a thick scum of filamentous algae which almost fill the water round the margins and can be seen extending down over the quickly shelving sides. A large *Enteromorpha* sp. also occurs in the pond where the stream of cold water flows into it.

At the edge of the water is a tussocky moss community including *Bryum* sp., *Webera* sp., *Drepanocladus revolvens* Warnst. and *Philonotis fontana* Brid. Some of these may grow submerged in the water, while behind stretches a more or less continuous moss mat supporting the following higher plants:

Equisetum arvense L. (sometimes growing in the pond)	a.
Phippsia algida (Soland.) R.Br.	f.
Cardamine pratensis L.	f.
Carex membranopacta L. H. Bail.	f.
C. bipartita All.	f.
Saxifraga cernua L.	o.
S. caespitosa L.	o.
S. rivularis L.	
Salix herbacea L.	

VIII. ERRATIC BOULDERS.

It has been mentioned that erratic boulders of mica schist are of more or less frequent occurrence on the plateau, while they may be further concentrated in number in the beds of the major watercourses. For a description of their vegetation the following types, affording somewhat different habitats, may be distinguished:

(*a*) Exposed.

(*b*) Sheltered, with snow covering in winter.

(*c*) In stream bed, variously disturbed by water and ice.

(*a*) *Exposed.*

These differ from the adjacent limestone rocks chiefly in being:

(1) Generally worn smooth by the action of the glacier which deposited them.

(2) Acidic instead of basic.

(3) Much less porous, and so holding water in the slightest crevice or depression.

(4) Very slowly weathered, and hence having a relatively static surface more easily colonised.

As a direct result of one or more of these ameliorating factors, we may get erratic pieces of mica schist half-covered with crustaceous lichens even when the surrounding limestone fragments are almost barren (see pp. 370—371). *Rhizocarpon geographicum* DC. var. *atrovirens* is about the most constantly important lichen on such exposed erratics, while *Lecidea* spp. (including the ubiquitous *L. goniophila*), *Candelariella vitellina* Müll. Arg., and others, are often associated. The types with a radially growing orange or yellow thallus are especially noticeable; against the light-coloured (often glaring white) background of barren limestone, the erratics show up dark, but with these bright crustaceous lichens they may have a peculiar "spotted-dog" appearance.

In some cases small erratics may show little sign of plant life, but the larger boulders even in the most exposed situations always support some crustaceous lichens, while a limestone surface under such extreme conditions may be perfectly barren. More often such larger erratics on the exposed plateau support a number of crustaceous lichens which may almost cover their surface, and in some cases there are a few hardy foliose and fruticose lichens and moss tufts on their damper and more sheltered sides. The plateau around may be occupied by poor *Dryas-Salix* polygon vegetation, being swept clear of snow in winter, as is the top of any outstanding boulder; but around its sides a small drift collects, as is shown by the close ground-shrub mat (p. 386) of *Cassiope* or *Empetrum* plants often to be found in its lee. Ptarmigan repair to such landmarks, whose tops are often littered with droppings; the resulting supply of nitrates doubtless affects the vegetation very favourably, but all the same these shrubs could hardly develop so well without a snow covering.

(*b*) *Sheltered.*

Although it was on the plateau, the example investigated quite obviously had a good snow cover in winter, except perhaps over its flat top. As the photograph shows (Pl. XXXIX, phot. 37), it lay in a slight depression covered with a snow-binding, hillock-tundra community (see Part II), and was itself extensively colonised by many species of plants—in places up to the angiosperm stage and always in striking contrast with the bare pieces of limestone seen in the foreground.

The earlier stages of colonisation are represented by crustaceous and other small lichens, the list including such interesting types as *Lecidea* and *Rhizocarpon* spp., and *Candelariella vitellina* with its powerful solvent action on rocks ((**13**), p. 393). These crustaceous lichens are of good growth and generally cover any area of the rock surface which is not already colonised by a higher life form.

In the early lichen stage, the most important are:

Candelariella vitellina Mull. Arg.
Lecidea goniophila Schaer.
L. griseoatra Schaer.
Placynthium asperellum Trev.

Rhizocarpon geminatum
R. geographicum DC. var. atrovirens
Ochrolechia tartarea Massal. var. frigida }
Physcia hispida Fr. } o.*

* Small plants.

A somewhat later lichen stage is evidenced on flat areas colonised by *Gyrophora hyperborea* Ach. with its conspicuous "black cups" ("*tripe de roche*"), while in places the *Physcia* and *Ochrolechia tartarea* may grow bigger and become more important and rapid accumulators of humus.

In a later stage, consisting mostly of foliose lichens, *Gyrophora hyperborea* is the chief plant, with much *Physcia hispida* and also *Ochrolechia tartarea.*

Following these comes *Orthotrichum speciosum* Nees. It is the chief dominant of any sheltered surface on the rock and particularly of any slight depression or crevice, from which its tussock can easily extend to occupy adjacent areas (**18**). The large tussocks of this moss, which show up well in the photograph (Pl. XXXIX, phot. 38), form a well-marked stage in association

Phot. 36. Persistent snow patch (on right) in August: the ground around it is barren. On left: pond, stream and late snow vegetation (p. 390).

Phot. 37. Large erratic boulder in damp depression with closed vegetation favoured by snow covering (p. 392), showing several stages of colonisation by plants. Background approaches "hillock tundra" type.

Phot. 38. "Close-up" of upper surface of erratic boulder: large tussocks of the moss *Orthotrichum speciosum* show up well (p. 392).

with certain luxuriant lichens which grow up with or upon the surfaces of the *Orthotrichum* tussocks.

MOSS
Orthotrichum speciosum Nees. d.

LICHENS
Ochrolechia tartarea Massal. (White powdery tufts (dry) in photograph)
Cetraria cucullata Ach.
C. islandica Ach. var. tenuifolia (crispa)
C. nivalis Ach. (White and feathery, extreme foreground of photograph)

The moss tussocks are hard and stick closely to the substratum. Holding mineral particles of weathered rock debris in their thick humous substance of matted roots, they form a nidus for colonisation by higher plants, which soon dominate them on the more sheltered sides of the boulder as is shown round the edges of the photograph. The first colonists, as might be expected, seem to be small grass-like sedges rooting in the tussocks. *Polygonum viviparum* is also frequent in this early stage, which is followed by a more stable community of *Dryas* and willows, though in places *Salix reticulata* was seen rooting in large moss-lichen tussocks without the intervention of any herb stage.

The following mosses and lichens also occurred on the rock surface of this one boulder:

BRYOPHYTES
Hypnum revolutum Lindb.
Orthothecium chryseum (Schwaegr.) B. and S.

LICHENS
Cladonia pyxidata Hoffm. var. pocillum Wain. (and probably type)
Lecidea pantherina Th. Fr.
Parmelia saxatilis f. purpuracea Schaer.
Thamnolia (Cerania) vermicularis S. F. Gray

(c) *Of stream bed.*

Not only do the streams and watercourses of the island vary greatly in type, but they also vary in duration. The most familiar type is that in which the stream has cut a deep ravine through the cliffs, as seen all round the island. These ravines, though they are often dry in August and September, have a bed strewn with smooth, water-worn boulders almost devoid of vegetation (see p. 377). There may be a few tiny close-growing moss tussocks or crustaceous lichens, or there may be no plants at all: the whole bed is too much disturbed every spring by the great rush of melting snow water (which presumably may last well into the growing season) to permit the establishment of higher vegetation.

Another familiar type of stream bed is open and strewn with dark erratic boulders as seen in Pl, XXXIV, phot. 22. Here again the erratics are smooth and almost barren though the bed supports but a trickle of water; once more the barrenness must be due to the rush of water coming down at the melting of the snows, for these watercourses drain a considerable area and must carry down a great bulk of water derived from the later-melting patches of snow and ice. The remains of one patch, melting very slowly, is seen in the mouth of a ravine on the right of the photograph (Pl. XXXIV, phot. 22) which was taken in early September.

Much less disturbed are the beds of the frequent small streams in the narrow valleys inland. The valley sides have static screes of the drier, poorer type described on pp. 379–80, for the stream is never torrential though its height must fluctuate considerably. The sides of an erratic boulder facing up-stream are however more completely barren just below the top than even the lower zones facing downstream, showing that the stream may at times swell to this higher level, when the rush of cold water or the grinding action of its floating ice fragments will shear off any crustaceous lichens which may have settled.

Such an erratic boulder is seen in Pl. I, phot. 2 (Part II); it is of the usual mica schist and stands up about 5 ft. from the bed of the stream. In the more permanent part of the stream certain algae are present, but the dry bed close to the boulder is quite barren. The bottom foot of the boulder is also devoid of plant life, being presumably washed by swift waters until late in the growing season; but the sides above, especially on the sheltered parts facing downstream, are colonised by crustaceous species of *Lecanora*, chiefly *L. calcarea** Sommerf. and *L. lacustris* Th. Fr. Their growth is often remarkably good considering the difficult conditions; some of the radial patches are 2 in. in diameter and must have withstood the action of water and ice for many years (cf. **19**).

Towards the top these denuding actions are less lasting and the surface, except for the exposed part facing upstream, is half-covered by the following lichen colonists:

*Lecanora calcarea Sommerf.
L. gibbosa Nyl.
L. lacustris Th. Fr.
Rhizocarpon geographicum DC. var. atrovirens
Gyrophora proboscidea Ach.

The top of the boulder was almost covered with lichens and is probably rarely if ever submerged under water or ground by ice. Nevertheless the lichens are of poor growth, probably because of an absence of winter snow covering in this shallow and windy valley. This inference is borne out by the poorly covered sides of the valley, occupied only by scattered *Cetraria nivalis*. The boulder was ancient and waterworn, so that no definite chomophytic communities were recognisable; but it was noticeable that the majority of the lichens grew much better in whatever small crevices or depressions they could find, suggesting again that outside such crevices and depressions the adverse factors were extreme.

The following is a full list of the lichens which almost covered the top of the boulder, the chief being the two species of *Gyrophora* which are noted silicicolous types of northern regions, and the orange coloured crustaceous *Rhizocarpon*.

Gyrophora proboscidea Ach.
G. cylindrica Ach.
Rhizocarpon geographicum DC. var. atrovirens
*Lecanora calcarea Sommerf.
Lecidea griseoatra Schaer.
Caloplaca elegans Th. Fr.
Alectoria ochroleuca Nyl.

* The only specimens found on the island were these, growing on this non-calcareous erratic!

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(*To be continued.*)

THE INFLUENCE OF PLANTS ON THE CONCENTRATION OF HYDROGEN IONS IN THE MEDIUM

By ANIELA KOSLOWSKA.

(*With fifty Figures in the Text.*)

I. THE SUBJECT-MATTER OF THE RESEARCH.

RESEARCH on the concentration of hydrogen ions in the soil water, in relation to the occurrence of single species and also of plant associations, has become one of the most productive lines of work in the modern sociology and geography of plants. Works in this sphere, growing more numerous every year, show two main directions of investigation. The first, most frequent and widespread, is the direct examination of the soil. Most sociological researches, independently of the school to which they belong, bear witness to the constantly repeated dependence of individual plant associations on the degree of acidity of the substratum. Furthermore, we possess a whole series of special works which indicate, on the basis of numerous observations, the exact limits of the degree of acidity within which particular species can develop. The second direction is represented by experimental works, confirming the results of the first by the aid of water and sand cultures of a whole series of species in conditions determined beforehand.

The general result of these numerous experiments and observations is the following: (1) the existence of a series of species showing the optimum of their development at a certain constant pH value, and (2) the constant dependence of the occurrence of certain plant associations on soil with a constant pH value.

The concentration of hydrogen ions in the soil appears to occupy the first place in an immense complex of edaphic factors decisive for the development of the flora of any given area.

With regard to the causes which produce these relations there exists in the literature a certain discordance. Some authors surmise that the influence on plants of the degree of concentration of hydrogen ions in the soil does not lie in their immediate action on the living organism, but rather in the dependence of the plant cells on changes occurring in the chemical processes of the soil, processes which are themselves conditioned by its acid or alkaline reaction.

Hartwell and Pember (**8**) consider that the influence of pH depends indirectly either on the lack of, or on the existence of, aluminium ions in the soil. In acid soils the aluminium ions prevent the growth of the so-called "alkaline plants." Bear (**3**) and others state that the division of plants into "acid" and "alkaline" species depends on the ability of certain plants to absorb from the soil ammoniacal salts derived from humus which does not yield to the process of nitrification, while other species absolutely need the nitrates in which alkaline soils abound. The abundance of mineral salts in the soil has also been recognised as a factor tending to mitigate the immediate influence of the acidity.

Lindquist (**12**), in his detailed studies on the ecological factors of beech forest, remarks that the occurrence of the so-called "acid" plants depends on the possibility of the production by their roots of a mycorrhiza exclusively connected with acid humus. On the other hand, for plants occurring on neutral or alkaline soils, this author accepts the immediate influence of the alkaline reaction or of a weakly acid one, independently of the nature of the soil and the degree of its nitrification. The same point of view, but only in respect of plants occurring on an acid substratum, is accepted by authors of classical works on this subject, such as Chodat (**4**), Mevius (**15**, **16**) and particularly Olsen (**17**). On the basis of experimental work and observations, they assert that, not secondary factors, but the immediate concentration of hydrogen ions in the soil has a decisive influence upon the floristic composition of the vegetation of given areas.

The acceptance of a dependence of such a kind suggests the possibility of investigating the properties of plants themselves on which the development of different concentrations of hydrogen ions depends. The present work aims at demonstrating this kind of biological character. The statement, as exact as possible, of the manner in which the living plant acts upon the concentration of hydrogen ions in the surrounding medium was the object of the experiments described below.

The power of the plant to change the reaction of its surroundings, long ago known to physiologists, has not hitherto been determined over a wide range of species, so as to define the biological peculiarities of different species in this respect. It is true that we have an abundant literature dealing with the chemical substances secreted by the root hairs (**11**, vol. **1**, pp. 280–1), as well as a great deal of discussion of the theory of exchange of anions and kations between the cell sap and an external liquid (**11**, vol. **2**, p. 63). But such work based on experiments with cultivated plants has not served to define precisely the physiological differences between species which might explain their occurrence under different natural conditions, i.e. their membership of certain associations or their attachment to particular conditions of the soil.

With regard to the question of the immediate influence of plants upon the *p*H of the surrounding, which interests us specially, the works of Miss Stelmach and Ulehla deserve to be considered. Miss Stelmach (**26**) gives, for two different species of *Sphagnum*, the changes of acidity occurring at two different constant *p*H values. The work of Ulehla (**28**) is more detailed, but the author employs somewhat different methods and therefore touches rather different problems.

He does not examine the reaction of the underground organs of plants to different *p*H values of the surrounding medium, but immerses sections of the living tissue of *Opuntia* in liquids of definite hydrogen-ion concentrations, and finds that they change the acidity to a certain constant *p*H value.

II. METHOD OF THE WORK.

In the experiments described below the author has taken plants directly from the ground in various soil conditions and immersed them in liquids of different degrees of *p*H.

The liquids used for the experiments had to conform to the following conditions. The distilled water must contain nutrient salts corresponding as far as possible to those of the soil, and in the greatest possible dilution. We know that the vital processes connected with the absorption of salts are directly related to the dilution of the liquids employed (**11**, vol. **2**, pp. 66, 70). It is also an established fact that the water circulating in the soil has an exceedingly small percentage of dissolved salts, many times smaller than that of Knop's nutrient solution. In order to obtain solutions approximating to this concentration I have taken a content of 0·04 gm. nutrient salts to 1 litre of water. But these solutions have to be sufficiently buffered, so that the CO_2 from the air constantly dissolving in them has no influence on the change in their hydrogen-ion concentration.

In order to find solutions possessing these properties I carried out some preliminary comparative experiments. In the first series of these the full solution of Knop diluted to 0·04 gm. per litre was used. By the gradual addition of drops of decinormal HCl and decinormal NaOH, I obtained a series of solutions of reaction varying from *p*H 3 to 8. A second series of nutrient solutions was arranged in the same manner, but with this difference, that the acid phosphate of sodium (Na_2HPO_4) of a concentration possessing the properties of a buffer, was used as a nutrient. 200 gm. Erlenmeyer flasks, each filled with 80 c.c. of nutrient solution, were employed for the experiments.

The plants designed for the experiments were prepared in the following manner. Specimens were taken from plant associations as typical as possible, generally in flower, together with the earth round them, and brought to the laboratory quite fresh. Then the root system was carefully rinsed under the tap until it was free from the tiniest particles of earth and finally washed in distilled water[1]. The specimens were then put into separate flasks so that the whole root system was immersed in water, while the shoot with leaves and flowers was in the air. Three series of flasks containing solutions ranging from

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[1] The procedure employed inevitably entailed a certain amount of damage to the root hairs and sometimes to the roots themselves. But despite this fault of the method the results showed a regularity which implied that the damage did not interfere with the reaction investigated. The aquatic plant *Hydrocharis morsus ranae*, which did not of course suffer this damage, showed reactions quite similar to those of the species taken from soil.

pH 3 to 8 were used for each species: where the available number of specimens was small two series were put together. Flasks with control solutions without plants were also set up for each series of experiments.

The pH values were determined by means of the quinhydrone method, the electrometrical "Cambridge Hydrogen-ion Apparatus" being employed. Each experiment lasted 5 days, during which the acidity of the solutions was measured every 24 hours.

With the same species of plants Knop's full nutrient solution showed the same changes as the solutions in which acid phosphate of sodium was used as a buffer for a wide range of pH values. When the concentration was ten times as great, however, the change in the degree of acidity in particular solutions did not occur.

In the control experiments changes of pH under the influence of the air occurred very easily in the unbuffered liquids with Knop's solution in long-continued experiments. For this reason I adopted the solutions in which the nutrients were supplied together with the acid phosphate of sodium in a dilution of 0·04 gm. for 1 litre. This concentration was slightly increased in certain solutions by the addition of drops of 1/10 N HCl and 1/10 N NaOH. The experiments were further continued in the manner described above.

III. SCOPE AND COURSE OF THE EXPERIMENTS.

During two periods of vegetation thirty-nine species of plants belonging to different plant associations were examined. The experiments were set up several times for a series of species in relation to their occurrence on various types of soil of different degrees of acidity. In addition parallel garden cultures were carried on. The same methods were applied to plants grown from seeds gathered in the field and cultivated on garden beds. As stated above, each experiment lasted 5 days and the acidity was measured every 24 hours.

Independently of the degree of change of reaction the experiment showed remarkable conformity in the rapidity of the reaction. After the first 2 days from the moment of setting up of the experiment the highest degree of alkalisation (or of acidification) was attained and this lasted, with but small variation, during the following days. Irregularities in this behaviour appeared only if the nutrient was attacked by fungi, when the liquids grew turbid and the results of the experiment were neglected. The length and the number of roots of the experimental plants had no influence on the course of the reaction. The alkalisation or acidification of the solutions occurred with equal rapidity with a single rhizome of *Anemone nemorosa* or with a rhizome of *Mercurialis perennis* provided with numerous lateral roots.

Most of the results are presented in the form of graphs. Subjoined are two full numerical tables to illustrate the run of changes with two species, *Vaccinium myrtillus* and *Corydalis cava,* which are totally different in their reaction on the medium.

Vaccinium myrtillus, *from coniferous forest, Przybystawice, district of Miechów* (pH *of the soil* = 4·5), *grown in a series of solutions of constant* pH *values, and showing* pH *changes on successive days.*

Experiment set up 16. vi	17. vi	18. vi	19. vi	20. vi
Solution of *p*H 2·5				
Without plants	2·5	2·5	2·5	2·5
Exp. 1	2·5	2·5	2·5	2·5
Exp. 2	2·5	2·5	2·5	2·5
Solution of *p*H 3·5				
Without plants	3·5	3·5	3·5	3·5
Exp. 1	3·5	3·5	3·5	3·5
Exp. 2	3·5	3·5	3·5	3·5
Solution of *p*H 4·1				
Without plants	4·1	4·1	4·1	4·1
Exp. 1	4·1	4·1	4·1	4·1
Exp. 2	4·2	4·2	4·1	4·1
Solution of *p*H 6·3				
Without plants	6·3	6·3	6·3	6·3
Exp. 1	6·2	6·1	6·1	6·1
Exp. 2	6·3	6·2	6·1	6·1
Solution of *p*H 7·4				
Without plants	7·4	7·4	7·4	7·4
Exp. 1	6·7	6·5	6·4	6·4
Exp. 2	6·5	6·4	6·4	6·4

Corydalis cava, *from deciduous forest at Cieszyn with* Acer campestre *and* Fagus silvatica (*p*H *of soil* 6·0).

Experiment set up 25. iv	26. iv	27. iv	28. iv	29. iv
Solution of *p*H 3·4				
Without plants	3·4	3·4	3·4	3·4
Exp. 1	4·0	5·5	6·2	6·3
Exp. 2	4·5	6·0	6·5	6·6
Exp. 3	4·3	5·8	6·4	6·5
Solution of *p*H 4·0				
Without plants	4·0	4·0	4·0	4·0
Exp. 1	6·0	6·1	6·5	6·6
Exp. 2	6·0	6·1	6·5	6·6
Exp. 3	5·7	6·2	6·5	6·6
Solution of *p*H 6·2				
Without plants	6·2	6·2	6·2	6·2
Exp. 1	6·5	6·5	6·7	6·7
Exp. 2	6·4	6·4	6·8	6·8
Exp. 3	6·5	6·5	6·8	6·8
Solution of *p*H 7·0				
Without plants	7·0	7·0	7·0	7·0
Exp. 1	7·0	7·0	7·0	7·0
Exp. 2	7·0	7·0	7·0	7·0
Exp. 3	7·0	7·0	7·0	7·0
Solution of *p*H 7·6				
Without plants	7·6	7·6	7·6	7·6
Exp. 1	7·5	7·5	7·5	7·5
Exp. 2	7·5	7·5	7·5	7·5
Exp. 3	7·5	7·5	7·5	7·5

IV. THE SPECIES INVESTIGATED AND THEIR ASSOCIATIONS.

(1) *Species characteristic of beech forest* (*Fagetum silvaticae*).

The beech association is one of the plant communities whose sociology is particularly well known. Numerous authors agree as to the general characteristics of the association and the distinction of the so-called "characteristic species" (**10**, **23**, **24**, **25**).

Among forest associations Fagetum silvaticae possesses the extreme type of soil in the direction of relative alkalinity. According to the investigations of Szafer (**27**) and of Sokołowski (**25**), the acidity of the humus in a beech forest oscillates most frequently between *p*H 6 and 5·4, but there are variations both in the direction of a stronger alkalisation, which on a calcareous substratum may attain *p*H 7·6, as well as of a stronger acidity, reaching in exceptional cases *p*H 3·7. The wide limits of the *p*H value relate primarily to the occurrence of the beech itself, while characteristic species associated with it occur within much narrower limits. According to the investigators mentioned above (**23**, **24**) and the author (**10**), the species cited below are primarily characteristic of Fagetum silvaticae: in the Polish lowlands, *Corydalis cava*, *Dentaria glandulosa*, *D. bulbifera*, *D. enneaphyllos*, *Asperula odorata*, *Mercurialis perennis*, *Galanthus nivalis*, *Veronica montana*, *Allium ursinum*; characteristic in a smaller degree are such species as *Anemone ranunculoides* and *Hacquetia epipactis*; locally, *Impatiens noli-me-tangere* and others. The greatest accumulation of the above-mentioned species appears at the optimum of development of the association, where the *p*H of the soil oscillates between 5·6 and 7. Some of them, however, as for instance *Allium ursinum*, which forms particular facies often passing into a community with dominant alder (*Alnus glutinosa*), grow generally in a rather more acid soil (*p*H 5·0).

Among the species cited as characteristic the following were experimentally investigated: 2-year old beech seedlings, *Corydalis cava*, *Asperula odorata*, *Mercurialis perennis*, *Dentaria glandulosa*, *Veronica montana*; also *Hacquetia epipactis* which appears locally in the west, and lastly *Allium ursinum*. The species were taken from various places in the field, from soil of different degrees of acidity, varying from *p*H 4·8 to 6·8. *Corydalis cava*, *Mercurialis perennis*, *Asperula odorata* and *Dentaria glandulosa*, however, taken from various soil conditions, showed a striking conformity in their reactions on particular solutions. As the curves (Figs. 1, 2, 3, 4) indicate, the strongly acid solutions below *p*H 3 yielded only a slight alkalisation; on the contrary, solutions of a higher *p*H value, 3·4 and more, yielded a strong alkalisation reaching in particular cases *p*H 6·4, 6·6, 6·8. The initial solution *p*H 8 yielded the very slight acidification of half a *p*H degree in the cases of *Mercurialis perennis* and *Asperula odorata*. Plants immersed in a solution of *p*H 7·5 did not change at all. *Veronica montana* differs very slightly from the other four preceding species in its manner of reacting on the solutions; the acid solutions are alkalised some-

FIGS. 1–48 show graphically the changes brought about in the hydrogen-ion concentration of culture solutions of different pH values by plants of different species, each experiment lasting 5 days. The abscissae represent the pH values at the beginning of each experiment, the ordinates the corresponding value at the end. The diagonal straight line therefore represents a base line corresponding with no change at any pH value, the circles indicating the initial pH values of the solutions used. The ordinates cut off between this base line and the corresponding point on the curve therefore represent the actual change occurring in each solution of given initial pH value. The horizontal broken line represents the pH value of the soil from which the plant was taken.

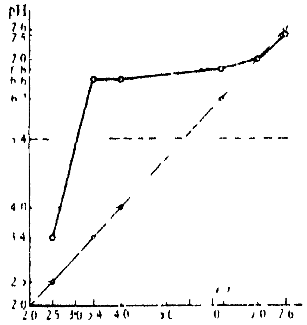


FIG. 1.

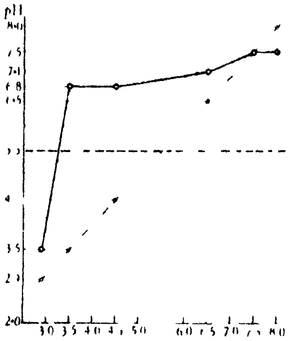


FIG. 2.

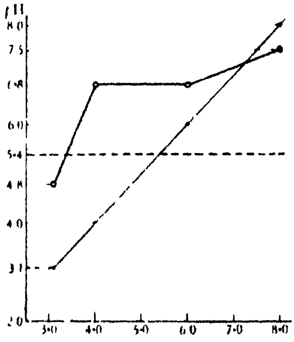


FIG. 3.

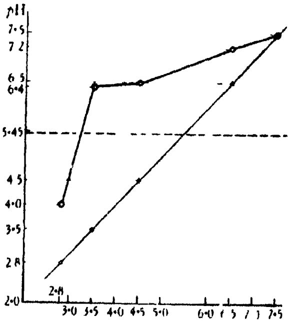


FIG. 4.

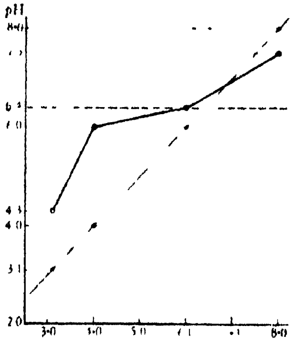


FIG. 5.

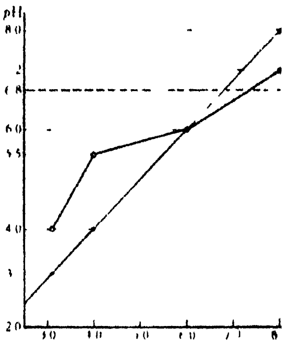


FIG. 6.

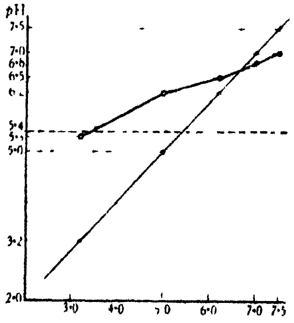


FIG. 7.

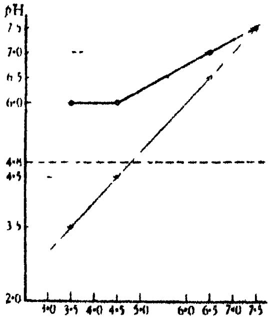


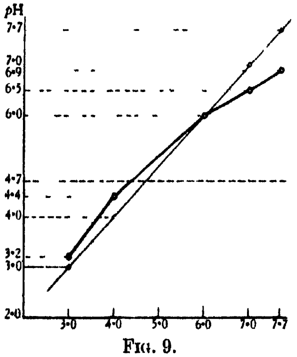
FIG. 8.

what more feebly; their degree of dissociation is brought to *p*H 6; the alkaline solutions are kept on the same level, *p*H 7·5 (Fig. 5). The beech seedlings show an analogous curve (Fig. 8). *Hacquetia epipactis* shows a rather slighter aptitude for alkalisation than the preceding species (Fig. 7). On the other hand, *Allium ursinum*, the species last examined, differs more from the type; it alkalises the acid solutions only up to *p*H 5·5, and acidifies the alkaline ones up to *p*H 7·2 (Fig. 6).

The result of this investigation is concordant in its principal features with the conditions in which these species occur in our area. The first four species, in particular *Corydalis cava* and *Dentaria glandulosa*, are generally dominant in the optimal facies of development of the association when the degree of acidification of the soil, especially on a calcareous substratum, is very slight, or even when the soil is weakly alkaline. The aptitude for alkalising acid liquids is quite comparable. *Veronica montana*, although a species which appears most rarely beyond the limits of the beech association, does not grow in a strongly alkaline facies on a calcareous substratum, but on the contrary, is a species frequently met with in the mountainous forest facies of the Carpathians with *Picea* dominant on sheets of detritus which are, of course, somewhat more acidic. The beech, *Fagus silvatica*, has a wide range of occurrence, depending on the *p*H of the soil. Neither of these species shows so high a power of alkalising solutions as do the four first-mentioned species. *Hacquetia epipactis* is a species characteristic of deciduous forests in general, sometimes occurring also in coniferous forests; it therefore shows a wider range of occurrence than the preceding species. But in their general character the curves of these seven species demonstrate a far reaching analogy. *Allium ursinum* alone differs rather remarkably from the type. As noted above, it is a species which in general characterises a facies with a humus more strongly acidified than the optimal facies of Fagetum silvaticae with *Corydalis cava* dominant.

According to the researches of Lindquist (**12**), the species characteristic of the Swedish beech forest vary within the following *p*H ranges. *Fagus silvatica* has the widest range, from *p*H 4·4 up to 8, *Asperula odorata* from 4·5 to 7·6, *Corydalis cava* within narrow limits from 6 to 7·5, and *Mercurialis perennis* from 6·5 to 8·3. *Allium ursinum* occurs more on the acid side, from 5·4 to 7. These facts correspond well with the results of our researches, *Asperula odorata* alone showing a wide range in Sweden while in our experiments it shows a type of curve similar to that of *Corydalis cava.*

FIG. 1. *Corydalis cava* (L.) Schwg. et K. Leafy forest with beech near Cieszyn, *p*H 5·4.
FIG. 2. *Mercurialis perennis* L. Beech forest on M. Klimczok, near Bielsk, *p*H 5·5.
FIG. 3. *Asperula odorata* L. Beech and fir forest near Cieszyn, *p*H 5·4.
FIG. 4. *Dentaria glandulosa* W.K. Beech forest near Cieszyn, *p*H 5·45.
FIG. 5. *Veronica montana* L. Beech thickets on M. Tul in the Silesian Beskid, *p*H 6·4.
FIG. 6. *Allium ursinum* L. Beech thickets on M. Tul in the Silesian Beskid, *p*H 6·8.
FIG. 7. *Hacquetia epipactis* (Scop.) D.C. Deciduous forest near Cieszyn, *p*H 5·7.
FIG. 8. *Fagus silvatica* L. Beech and fir forest on M. Klimczok, near Bielsk, *p*H 4·8.



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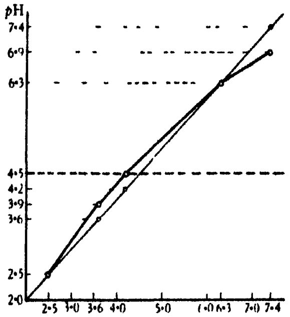

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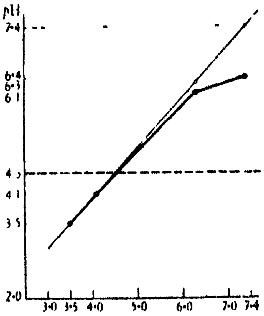

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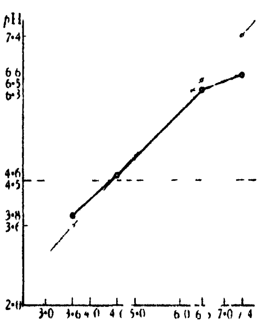

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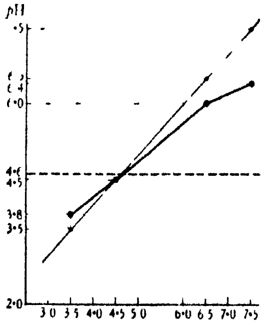

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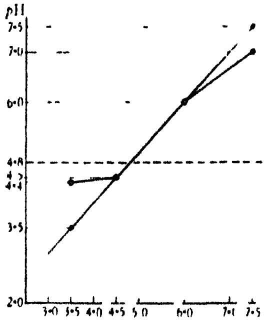

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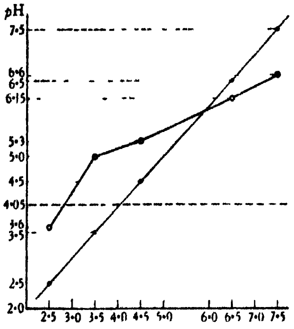

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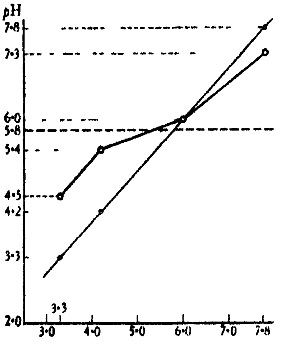

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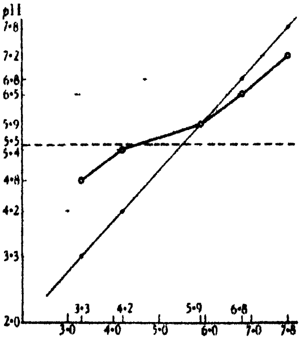


FIG. 17.

FIG. 9. *Pinus silvestris* L. Pine forest near Mikołów, on a sandy substratum, *p*H 4·7.

FIG. 10. *Picea excelsa* L.K. Piceetum, Przybysławice, in Miechów district, on a loamy substratum, *p*H 4·5.

FIG. 11. *Vaccinium myrtillus* L. Spruce forest, Przybysławice, *p*H 4·5.

FIG. 12. *Trientalis europaea* L. Spruce forest on a loamy substratum, Przybysławice, *p*H 4·5.

FIG. 13. *Potentilla tormentilla* Neck. Pine forest, Borek Fałęcki, *p*H 4·6.

FIG. 14. *Majanthemum bifolium* (L.) D.C. Fir and spruce forest near Bielsk, *p*H 4·8.

FIG. 15. *Anemone nemorosa* L. Pine forest, Borek Fałęcki, *p*H 4·05.

FIG. 16. *Luzula pilosa* (L.) Willd. Pine forest in the desert Błędowska, *p*H 5·8.

FIG. 17. *Paris quadrifolia* L. Pine forest in the desert Błędowska, *p*H 5·5.

(2) *Species characteristic of coniferous forests* (Pinus silvestris *and* Picea excelsa *dominant*).

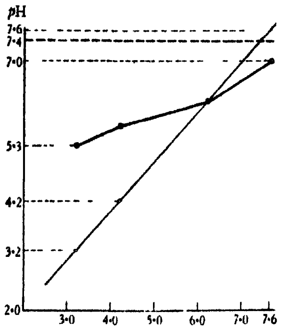
The pine forests, Pineta, and the associations with spruce (*Picea excelsa*) dominant, are characterised by very acid humus, from *p*H 3·8 to 4·8, thus presenting a strong contrast to the Fageta.

Two-year-old seedlings of pine (*Pinus silvestris*) and of spruce, together with four species remarkably characteristic of these associations, *Vaccinium myrtillus*, *Trientalis europaea*, *Potentilla tormentilla* and *Majanthemum bifolium*, were used for the experiment. The plants were taken from various places in the field, but the acidity in all cases was almost identical, varying from *p*H 4·5 to 4·8. The curves obtained (Figs. 9–14) show a far-reaching conformity of reaction on particular solutions. Acid solutions from *p*H 3 upwards either do not change at all, or are very feebly alkalised; alkaline and nearly neutral solutions down to *p*H 6 are acidified and reach neutral or feebly acid values. Apart from these fundamental characteristics certain small individual differences are seen in particular species: *Vaccinium myrtillus* did not alkalise acid solutions at all, but acidified alkaline solutions very strongly (Fig. 11); the remaining species changed imperceptibly, reacting in the direction of alkalisation (Figs. 9, 10, 12, 13). *Majanthemum bifolium* showed the strongest reaction and acidified alkaline solutions most feebly (Fig. 14). According to the investigations of Lindquist (**12**) and Olsen (**17**) in the forests of Sweden and Denmark, these species occur within the following limits: *Vaccinium myrtillus* from *p*H 3·8 to 4·8; *Trientalis europaea* and *Potentilla tormentilla* in very narrow limits from *p*H 4 to 4·5; *Majanthemum bifolium* as a rule, from *p*H 4·1 to 5, though it may occur rarely on a substratum reaching almost neutral values (*p*H 6·5). It results from these facts that *Vaccinium myrtillus* is a species able to grow in the most extreme conditions on the most strongly acid soil (*p*H 3·8); while *Majanthemum bifolium,* though it attains its maximum development in acid humus, also occurs with a *p*H of 6·5 and is thus not a species so closely attached to extremely acidic soils as the preceding ones. The curves resulting from our experiments confirm these observations.

(3) *Species occurring both in deciduous and in coniferous forests.*

Three species, *Anemone nemorosa, Paris quadrifolia* and *Luzula pilosa,* occurring commonly in both types of the forests previously described, were experimented with. These species have a very wide range of occurrence from strongly acidic soils attaining *p*H 4 to neutral, sometimes slightly alkaline in deciduous forests on a calcareous substratum.

The curves obtained from the experiments demonstrate for these three species a far-reaching analogy in their general character (Figs. 15–17). They represent a type evidently medial between the curves of the species of beech forests and those characteristic of coniferous forests. Solutions of *p*H 3·4



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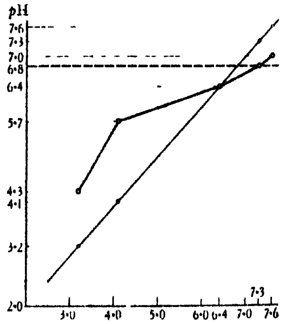

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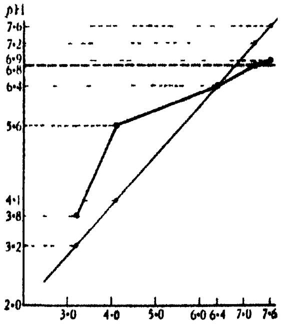

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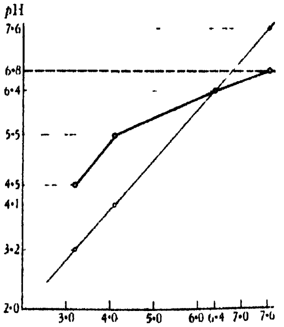

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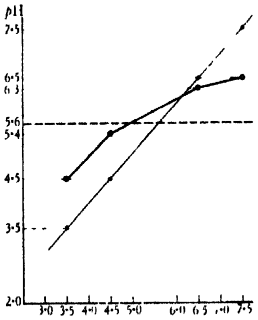

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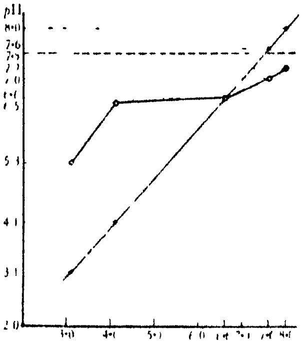

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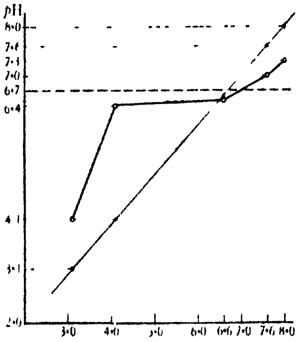

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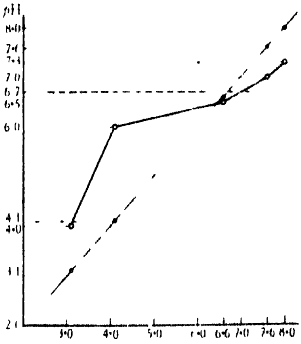

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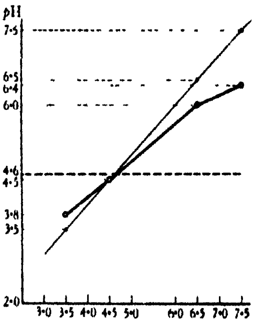

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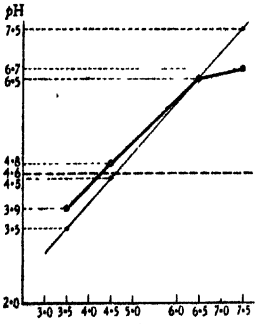

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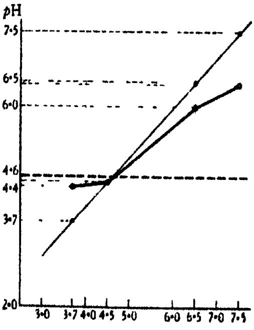

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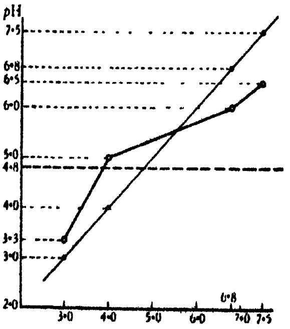


FIG. 29.

are alkalised to 4·8; alkaline solutions are acidified a little more strongly than by the species of beech forests, but more feebly than by those of coniferous forests.

(4) *Species of "low" peat-bogs ("low moor," "fen").*

In their typical development "low" peat-bogs possess a slightly acid to neutral reaction. The species of these communities, like those of forest associations can be placed in a series beginning with open water plants, water of neutral or sometimes even a feebly alkaline reaction, and ending with those which, like *Carex flava* for instance, pass to "high" peat-bogs ("Hochmoor") with *Sphagnum* of strongly acid reaction. I used five species, viz. *Hydrocharis morsus-ranae*, a plant of open waters taken from a pond of *p*H 7·1, *Eriophorum polystachium*, *Carex Goodenoughii* and *Valeriana simplicifolia* from the typical "low" peat-bogs, *p*H 6·8, and lastly *Carex flava* from a medial peat-bog, passing in places into a *Sphagnum* peat-bog of *p*H 5·6.

The character of the curves resulting from my experiments (Figs. 18–22) corresponds entirely to the range of occurrence in the field of the species cited. Alkaline solutions are very little acidified by *Hydrocharis morsus-ranae*, which alkalises most strongly the acid ones; on the contrary *Carex flava*, which acidifies alkaline solutions to *p*H 6·5, alkalises also very weakly acid solutions. *Carex Goodenoughii*, *Valeriana simplicifolia* and *Eriophorum polystachium* represent the medial type between the other two.

(5) *Species of granitic and calcareous soils in the Tatras.*

I have taken for my experiments first, species of the Caricetum firmae ("Firmetum"), an association characteristic of the calcareous soils of the Tatras, whose acidity varies between *p*H 5·3 and 6·8 (acidities above 6·0 occur most frequently); secondly species from the Juncetum trifidi, an association of the Tatra granitic soils which are remarkably acid, varying from *p*H 3·7 to 4; thirdly *Nardus stricta*, a species ranging in the mountain associations from *p*H 3·8 to 6·0. The results of the experiments showed a far-reaching conformity with the conditions in which these species occur in the field.

FIG. 18. *Hydrocharis morsus-ranae* L. Pond near Oświęcim, *p*H of water 7·4.

FIG. 19. *Carex Goodenoughii* Gay. Low peat-bog near Imielin, *p*H 6·8.

FIG. 20. *Eriophorum polystachium* L. Low peat-bog near Imielin, *p*H 6·8.

FIG. 21. *Valeriana simplicifolia* (Rchb.) Kab. Low peat-bog near Imielin, *p*H 6·8.

FIG. 22. *Carex flava* L. Transitory peat-bog in Borek Fałęcki, *p*H of soil 5·6.

FIG. 23. *Sesleria bielzii* Schur. Calcareous gravel in the Kondratowa valley, Tatras, *p*H 7·5.

FIG. 24. *Viola alpina* Jacq. Firmetum on calcareous substratum on Czerwone Wierchy, Tatras, *p*H 6·7.

FIG. 25. *Carex firma* Host. Firmetum on calcareous substratum, Czerwone Wierchy, Tatras, *p*H 6·7.

FIG. 26. *Juncus trifidus* L. Granitic substratum, Czerwone Wierchy, Tatras, *p*H 4·6.

FIG. 27. *Avena versicolor* Vill. Granitic substratum, Czerwone Wierchy, Tatras, *p*H 4·6.

FIG. 28. *Chrysanthemum alpinum* L. Czerwone Wierchy, Tatras, *p*H 4·6.

FIG. 29. *Nardus stricta* L. Open space in coniferous forest, Wisła, Silesian Beskid, *p*H 4·8.

The species of calcareous soils have shown their capacity for the alkalisation of acid solutions as strongly as the beech forest species; but they differ from the last by possessing a somewhat stronger aptitude for the acidification of alkaline solutions (Figs. 23–25). Of the three species examined *Carex firma* and *Viola alpina* were taken from the typical "Firmetum," while *Sesleria Bielzii* came from the calcareous gravel of an alkaline soil of *p*H 7·5; all three curves present a far-reaching analogy, *Carex firma* itself alone alkalising acid solutions somewhat more feebly than the two other species.

From Juncetum trifidi three species most characteristic for this association were taken for the investigations, *Juncus trifidus, Avena versicolor* and *Chrysanthemum alpinum.* The curves obtained from these experiments resemble in character the curves obtained for the species of coniferous forests; there appears in both a very insignificant capacity for the alkalisation of acid solutions, together with a rather remarkable ability for the acidification of alkaline solutions (Figs. 26–28). *Nardus stricta,* in accordance with the ubiquitous character of its occurrence, demonstrates in its curves medial properties between the calcareous and granitic species of the Tatras (Fig. 29).

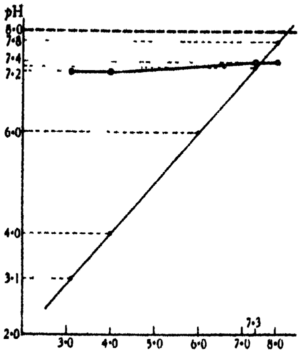
(6) *Species of steppe associations on a calcareous substratum.*

In order to complete the general review of various types of plant associations several species were examined which occur on the calcareous rocks of the Polish lowlands in the so-called "steppe associations" on the most alkaline type of soil.

From the southern slope of a Cretaceous hill, from the association Inuletum ensifoliae (soil *p*H 8), were taken three species growing near each other, *Festuca sulcata, Carex caryophyllea* and *Anemone silvestris.* Among these species, *Festuca sulcata* is the most characteristic of steppe associations on a calcareous substratum, *Carex caryophyllea* much less so, while *Anemone silvestris* passes also into scrub and communities of forest type. These three species acted on the *p*H value of the surrounding solution differently, corresponding to the conditions in which they occur in the field. *Festuca sulcata* showed the greatest power of alkalising acid liquids of any species tested up to the present, bringing the reactions to *p*H 7·2, 7·4 (Fig. 30). *Carex caryophyllea* showed a strong power of alkalisation, but not equal to that of the *Festuca* (Fig. 31). Finally *Anemone silvestris* presents in its curve the characteristics of medial species possessing a wide range (Fig. 32).

V. VARIABILITY IN THE CAPACITY OF A SPECIES TO CHANGE THE REACTION OF THE MEDIUM.

It has been shown that beech forest species from various soil conditions, where acidity varies between *p*H 5·4 and 6·8, alkalised the acid solutions in our experiments equally strongly, whatever the degree of acidity of their substratum.



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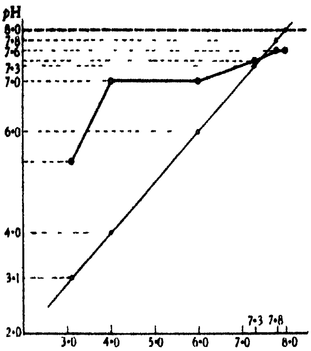

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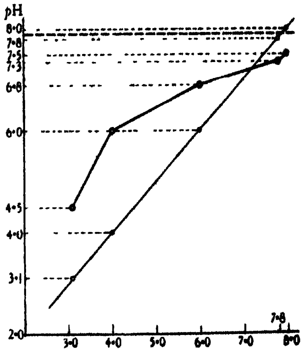

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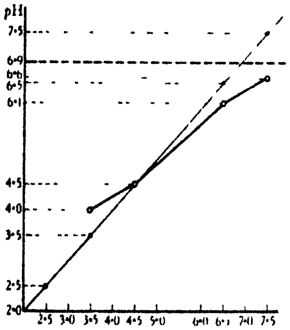

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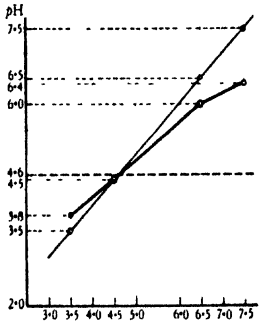

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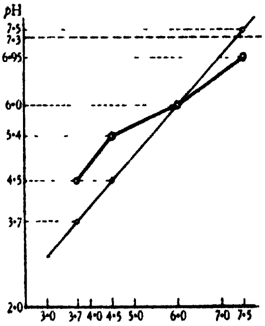

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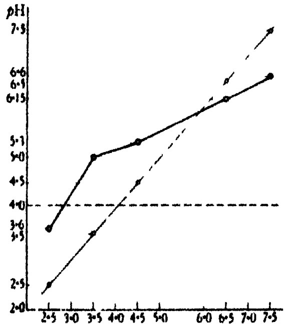

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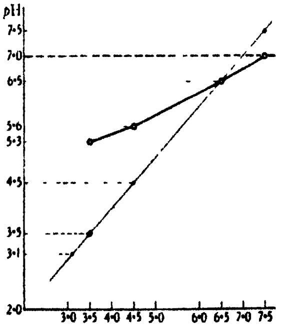


FIG. 37.

FIG. 30. *Festuca sulcata* (Hack.) Nym. Inuletum ensifoliae on a calcareous substratum, Miechów district, *p*H 8.

FIG. 31. *Carex caryophyllea* Lat. Inuletum ensifoliae on a calcareous substratum, Miechów district, *p*H 8.

FIG. 32. *Anemone silvestris* L. Inuletum ensifoliae, Miechów district, *p*H 7·9.

FIG. 33. *Azalea pontica* L. From a garden bed, *p*H 6·9.

FIG. 34. *Juncus trifidus* L. On granitic substratum, Czerwone Wierchy, Tatras, *p*H 4·6.

FIG. 35. *Juncus trifidus* L. Grown in garden for two years, *p*H 7·35.

FIG. 36. *Anemone nemorosa* L. Alder wood, Borek Fałęcki near Cracow, *p*H 4·05.

FIG. 37. *Anemone nemorosa* L. Garden bed, *p*H 7·0. (At *p*H 3·1 the plant withered.)

In order to ascertain whether species characteristic of associations developed on acid substrata act in the same manner, it was necessary to use garden cultures, since under natural conditions these species do not inhabit a wide range of soils like the beechwood species described above. *Azalea pontica* was chosen as a representative species of coniferous forest, since its occurrence is similar to that of such species as *Vaccinium myrtillus*, *Trientalis europaea*, etc. Among plants of the granitic soils of the Tatras *Juncus trifidus* was taken.

The seeds of *Azalea pontica* gathered in a pinewood in Volhynia, its natural station, were sown in a garden soil of *p*H 6·8. I chose for experimentation small plants 1½ years old with well-developed root systems. The curve obtained indicates that, although this species was growing in an almost neutral medium, its reaction was like that of species characteristic of coniferous forests, alkalising acid solutions very slightly but acidifying alkaline ones quite strongly (Fig. 33). This species, characteristic of the pine association, thus kept its primary property of reacting on the hydrogen-ion concentration of its medium, although the conditions under which it grew differed from the normal by nearly 3 degrees of acidity.

Juncus trifidus behaved somewhat differently. Grown for 2 years in a garden culture of *p*H 7·3, it showed a curve of the same general form, but alkalising acid solutions somewhat more strongly and acidifying alkaline ones more weakly, than did the plants grown in their natural conditions in granitic soil. Compared with *Azalea pontica*, *Juncus trifidus* (Figs. 34, 35) possesses a wider range of growth in the field, as it occurs outside the typical association in soil showing a *p*H of less than 4. It may be that this wide range of tolerance is the cause of the insensible change of the character of its curve in specimens grown in a feebly alkaline soil.

Subsequently a special investigation was made of the ubiquitous species possessing a wide tolerance of soil conditions: *Anemone nemorosa*, *Viola palustris* and *Convallaria majalis*.

Specimens of *Anemone nemorosa* were taken from very different soils; some from a humid alderwood (*p*H 4), others from a deciduous forest on a calcareous substratum (*p*H 7). The curves obtained, while similar in general character, differed in the degree of deviation: in the second case the alkalisation of acid solutions was stronger than in the first (Figs. 36, 37). At the same time a curious difference was noted in the action of the plants on strongly acid solutions. Specimens grown in a soil of *p*H 7, when immersed in a solution of *p*H 3 withered on the second day, while specimens grown in a soil of *p*H 4 tolerated a solution of *p*H 2·5 without any withering at all.

Viola palustris was taken from a "low" peat-bog (*p*H 6·8) and from a "high" peat-bog or "Hochmoor" (*p*H 4·6). The curves obtained from the two experiments showed remarkable differences (Figs. 38, 39).

Convallaria majalis—a species fairly characteristic of the acid substratum of coniferous forests, but apart from this possessing a wide range of tolerance—gathered from a pine forest (soil of *p*H 4·2) showed a curve similar to that of *Trientalis europaea*, etc. (Fig. 40). On the contrary *Convallaria majalis*, grown in a garden culture (*p*H 7), presented a curve showing far stronger powers of alkalisation than the one from acid soil (Fig. 41).

It results from these experiments that species occurring within narrow *p*H limits and characteristic of particular associations, possess more or less constant properties of reacting on the *p*H of the medium, and these are unchanged even when the plants are cultivated in artificial conditions of acidity, differing widely from the normal ones. On the contrary, ubiquitous species, while keeping the same fundamental character of the curves, show changes in the degree of reaction on the *p*H of the medium, depending on the soil from which the specimens are taken.

The establishment of the variability of the reaction on the concentration of hydrogen ions of the medium of the same species, grown in various soil conditions, suggested the necessity of examining whether this property is hereditary for particular individuals within the limits of the same species. With this aim in view, the following experiments were made. Three species of wide tolerance, *Anthoxanthum odoratum*, *Pinus silvestris*, and "micro-species" of *Festuca ovina*, were grown from the seeds of specimens found in the field and taken, for each particular species, from two extremely different soil conditions. The seeds were sown in the garden in identical conditions (*p*H 7–7·5).

Anthoxanthum odoratum, coming from a steppe in Rumania on a calcareous substratum, in the environs of Herkules Bad, on an alkaline soil up to *p*H 8, was sown and cultivated on a garden bed of *p*H 7. The same species from the granitic caps of Czerwone Wierchy (Tatras) (soil *p*H 4·2) was treated in the same way: flowering specimens were used for the experiments. The curves obtained from both experiments are identical (Figs. 42, 43), although the specimens grown from the seeds from Czerwone Wierchy were beyond comparison weaker and less well developed than the specimens from Rumania.

The experiments on the pine gave curious results. Two-year-old seedlings of pine, from a normally developed pinewood with acid humus, react on the *p*H of solutions like the other species characteristic of that association. Nevertheless, *Pinus silvestris* has a wide natural range of tolerance, often growing immediately on calcareous rock (Pieniny, Jurassic hills, Kraków-Wieluń). Seeds of pine growing on the calcareous rock at Macelak in the Pieniny, and of pine colonising the "high" peat-bog Niechrzczone, in the great forest of Niepołomice, were selected for garden cultures. The germinating pines were cultivated in pots in soil with a *p*H of 7·5. Just as for *Anthoxanthum odoratum*, the curves obtained in the two experiments presented no differences (Figs. 44, 45). But these curves differ fundamentally from those given by pine taken from a forest association normally developed (Fig. 46). Thus we observe in

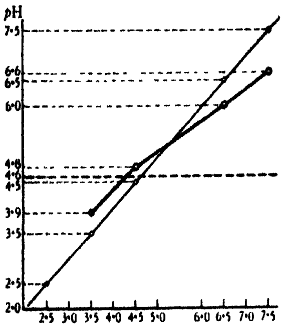
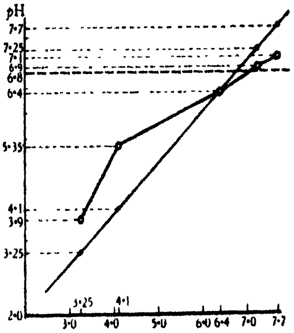


Fig. 38.



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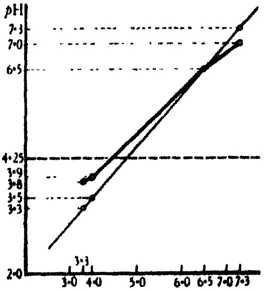

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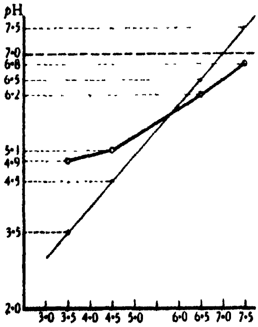

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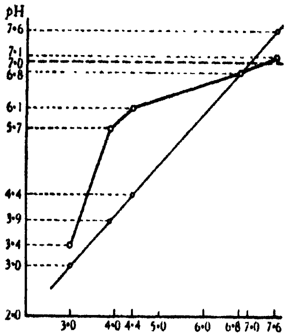

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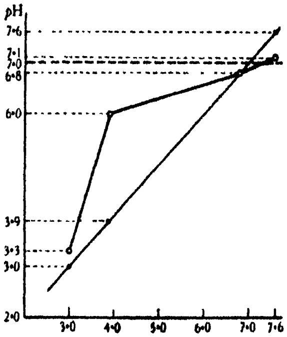

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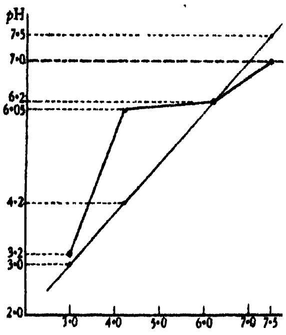

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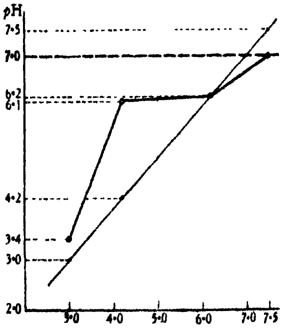

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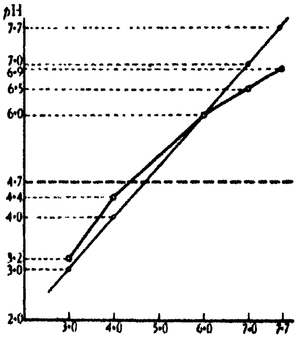

Fig. 46.

Fig. 38. *Viola palustris* L. High peat-bog, Borek Fałęcki, near Cracow, *p*H soil 4·6.

Fig. 39. *Viola palustris* L. Low peat-bog near Olkusz, *p*H soil 6·8.

Fig. 40. *Convallaria majalis* L. Pine forest on sandy substratum, Niepołomice, near Cracow, *p*H 4·25.

Fig. 41. *Convallaria majalis* L. Garden bed, *p*H 7·0.

Fig. 42. *Anthoxanthum odoratum* L. Garden culture of seeds from a steppe association on calcareous rock at Herkules Bad (Rumania), *p*H 7·0.

Fig. 43. *Anthoxanthum odoratum* L. Seeds from granitic substratum in the Tatras, taken from a soil of *p*H 4·2 grown in garden culture at *p*H 7·0.

Fig. 44. *Pinus silvestris* L. Seeds from a peat-bog in the forest of Niepołomice, grown in garden soil of *p*H 7·0.

Fig. 45. *Pinus silvestris* L. Seeds from calcareous rock in the Pieniny grown in garden soil of *p*H 7·0.

Fig. 46. *Pinus silvestris* L. Pine forest on sandy substratum near Mikułów.

this species a wide range of variability in reaction to the acidity of the medium, corresponding to the extremely different conditions in which the pine can develop.

The seeds of the Sheep's Fescue-grass (collective species, *Festuca ovina*) belonged to two segregate species which are closely allied, *Festuca glauca* and *F. vulgaris*. The seeds of the former, occurring exclusively on calcareous soils, were gathered on the calcareous rock of Ojców, soil *p*H 7·5. The seeds of *Festuca vulgaris*, which possesses a fairly wide range of tolerance but avoids alkaline soils, were gathered in a pinewood, soil *p*H 4·5. In garden culture both these species were grown in the same conditions, soil *p*H 7. The curves obtained are similar, but not identical: *Festuca glauca* alkalises more strongly in accordance with the conditions in which it appears in the field (Fig. 47); *F. vulgaris*, on the other hand, alkalises more feebly (Fig. 48). Here we are evidently concerned with closely related though distinct microspecies, and this is probably the cause of their having kept in garden culture the ability to react differently, while in the previously described species specimens gathered in different conditions showed no differences at all.

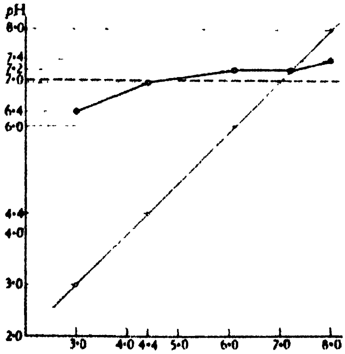

FIG. 47.

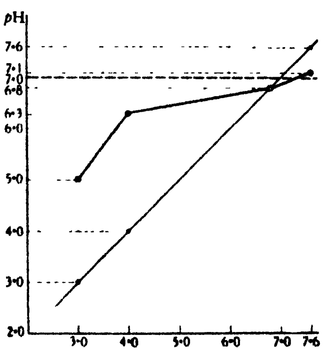

FIG. 48.

FIG. 47. *Festuca glauca* Lam. Seeds from calcareous rock in Ojców, grown in garden soil of *p*H 7.
FIG. 48. *Festuca ovina* var. *vulgaris*. Seeds from a pine forest, *p*H of soil 4·5, grown in garden soil of *p*H 7.

As a result of these experiments, it is evident that the change in action on the *p*H of the medium in ubiquitous species, being a physiological difference occurring within the limits of a single species, cannot be considered as hereditary.

Another point remained to be considered. Does this marked capacity for changing the reaction of the medium occur only at the time of flowering, or is it independent of this? I have already stated that in order to get comparable results the plants for experiment were as far as possible gathered during the same period of development, namely when they were in flower. This of course could not apply to the seedlings of beech, pine and fir; also the Tatra granitic species were examined in a barren state. The results show that the character of the curves, obtained from experiments on the seedlings and barren plants, does not differ much from that of the curves obtained from species examined in full bloom.

However, in order to investigate this matter directly I examined one species, *Festuca sulcata*, which showed the most extreme reactions, in three different periods of its development: in the vegetative spring stage, in the flowering period, and in autumn after the seeds had been produced. In all three cases I obtained a curve identical with the one shown in Fig. 30.

The concentration of hydrogen ions in the soil being in great measure the synthetic expression of the most important soil properties, is at the same time one of the most important factors determining the distribution of plant associations in the field. The search in the plants themselves for the causes of their reactions on the *p*H values of the medium, which are in direct relation to the conditions in which the different species occur, offers in most cases the possibility of causal explanation of the cardinal phenomenon in plant sociology, the so-called "characteristic" species in the associations. The more or less constant dependence of these species on a given community is in many cases most probably the expression of physiological properties corresponding with the narrow limits of the *p*H values of the soil characteristic of the community in question. The ubiquitous species, on the other hand, differ from the narrowly limited characteristic species in this very quality.

VI. AN ATTEMPT TO EXPLAIN THE PHENOMENA DESCRIBED.

The capacity for reacting on the acidity of the medium, specific for each species or for certain groups of species, should eventually find its explanation in the structure of the living organism, which is the outward expression of its physiological properties. Theoretically, we must accept two fundamental possibilities: the phenomena in question may be connected either with the semi-permeable properties of the plasma lining the cell, or with the quality of its sap.

According to Mevius (**15**) and Arrhenius (**2**), there exists an immediate connection between the *p*H value and the state of the living plasma in the cell. The investigation of the properties of the protoplasmic lining of the cell, on which depend various abilities of the living organism to absorb salts in dilute solution, has lately grown explicit by the establishment of the so-called isoelectric point of proteins which, according to the opinion of some contemporary investigators (Loeb (**13**), Robbins (**21**), Pischinger (**20**)), is one of the cardinal properties of the living cell, and makes clear a whole series of its essential physiological properties. Other scientists, as for instance T. Demidenko (**5**), discuss this matter without considering it as very important. The methods of investigation which aim at settling the *p*H value of the plasma in the living cell at its isoelectric point, if such methods are really valid, offer great difficulties, and in relation to our problems are absolutely impracticable (**22**). Therefore in my work I had to neglect them altogether.

As regards the investigation of the cell sap, we do not possess up to the present any methods in plant physiology which would permit a general investigation of the properties of the living cell without damaging its internal structure. The method of pressing out the sap from the living plant with a press, although exceedingly crude and inadequate, is nevertheless in certain cases the only method yet available. Numerous writers have stated that the concentration of hydrogen ions of the cell sap, examined in the cell *in vivo* as well as in the expressed cell sap, is not directly related to the *p*H of the medium (**14**). It thus becomes necessary to seek other properties which might make clear the above-described phenomena.

On the basis of physico-chemical laws, we may surmise beforehand that when strongly buffered solutions in which weak acids are united with strong bases, come into contact with exceedingly weak and feebly buffered solutions with an acid reaction, they must tend to "alkalise" them, i.e. reduce their acidity by transferring to them dissociated alkaline ions. In the phenomena described in this paper the most fundamental and important reaction is the ability to alkalise acid solutions shown by some species: the power of acidifying alkaline solutions, on the other hand, is comparatively weak, even in species such as *Vaccinium myrtillus*. The existence in plant cells of numerous organic phosphates as well as weak organic acids, and also of strong bases such as those of potash, soda, etc., suggests that the degree of buffering of the saps within the living cell may be considerable and directly correlated with the power of the plant to react on the acidity of the medium.

The established methods of examination of the degrees of buffering of the cell sap for various degrees of *p*H, and of drawing the so-called buffering curve ("buffer index curve") have often been applied in physiological work (**1**, **9**) and have been used in the present investigations.

In order to obtain a uniform opening of the cells, the subaerial parts of the plants investigated were triturated with sand in a mortar, and the sap expressed under a pressure of 150 atmospheres. The subsequent examination was carried out as quickly as possible to avoid a secondary reaction of the enzymes. To 4 c.c. of sap, whose degree of *p*H was examined by the electrometric method, 0·5 c.c. 1/10 *N* HCl was added until the acidity attained *p*H 2·5. In this manner the "titration curve" was obtained and the degree of buffering of the different degrees of *p*H calculated on the basis of the following ratio:

$$\text{Degree of buffering} = \frac{\text{Number of gm. of acid or base added to 1 litre of solution required to cause the ascertained change of } p\text{H}}{\text{Change of degree of } p\text{H}}.$$

From these data the curve of buffering was drawn, the abscissae representing the degrees of *p*H and the ordinates the corresponding degrees of buffering.

Three species characteristic of the beech association were examined in this way, *Corydalis cava*, *Mercurialis perennis* and *Dentaria glandulosa*, all of which strongly alkalise acid solutions: also *Anemone nemorosa*, a ubiquitous species which showed a medial curve in the previous experiments.

Mercurialis perennis and *Dentaria glandulosa* had a sap reaction exceeding[1] *p*H 8·5. Since it is impossible to obtain by the electrometric method exact evidence of such a high degree of *p*H, it was only from the moment when the change in the *p*H of the sap was brought by titration to *p*H 8 that exact results could be obtained. For this reason the curves of buffering are given only for *Corydalis cava* and *Anemone nemorosa*: for the other two species the c.c. of 1/10 *N* HCl required to acidify the sap to *p*H 2·5 are recorded.

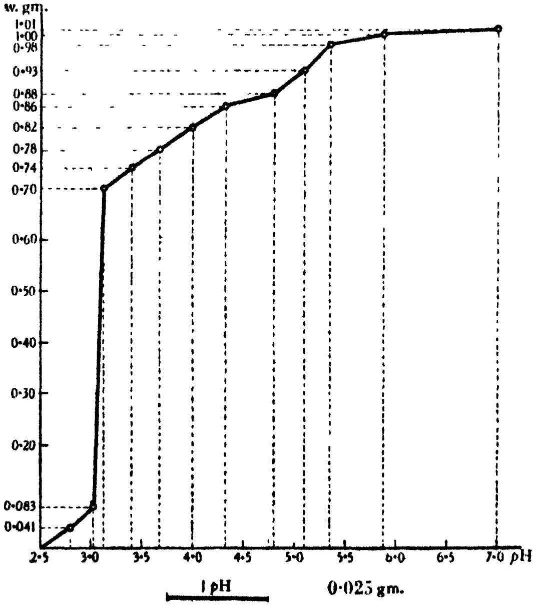

FIG. 49. Buffering of the sap of *Corydalis cava*. Abscissae = degrees of *p*H. Ordinates = corresponding degrees of buffering in gm.

The three beechwood species investigated showed a strong similarity in their degree of buffering. In all three cases the saps were very strongly buffered. For *Corydalis cava*, in order to bring 4 c.c. of neutral sap (*p*H 7) to *p*H 2·5, 6·5 c.c. 1/10 *N* HCl were necessary. At the same time, as the curve (Fig. 49) shows, the strongest buffering is at *p*H 3, and there is a second phase of very strong buffering at *p*H 2·5, but this was not included in the graph nor in the figures of c.c. of 1/10 *N* HCl. *Mercurialis perennis*, whose sap, as already remarked, is very strongly alkaline (above *p*H 8·5), required 8·5 c.c. of 1/10 *N* HCl to bring its 4 c.c. to *p*H 2·5. Here again the strongest buffering appears in decidedly acid solutions. In *Dentaria glandulosa* as much as 11 c.c. of

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[1] Although the experiment was carried out as quickly as possible after expressing the sap, it may be that the high *p*H value should in these conditions be ascribed to the secondary enzymatic reactions.

1/10 *N* HCl are required in order to bring the strongly alkaline sap to the same *p*H 2·5.

Anemone nemorosa differs fundamentally from these three species. Possessing a weakly acid, nearly neutral sap reaction (*p*H 6·6), it requires only 3·5 c.c. of 1/10 *N* HCl in order to bring its acidity to *p*H 2·5 (Fig. 50), and thus shows a feeble buffering, strongest at *p*H 4. In comparison with *Corydalis cava,* whose sap reaction only differed by 0·4 *p*H, *Anemone nemorosa* shows on the whole a degree of buffering of the sap not much more than half as great. In connection with these facts a curious detail was observed while the experiments were being carried out. *Corydalis cava* placed in a liquid of *p*H 2·5 has only a slight power of alkalisation, but nevertheless it continues alive in spite of the violent change of conditions. *Anemone nemorosa,* on the other hand, taken like *Corydalis cava* from a soil of neutral reaction, and placed in a solution of *p*H 3·1, withers the next day. But if it has grown in an acid soil, it shows a stronger resistance.

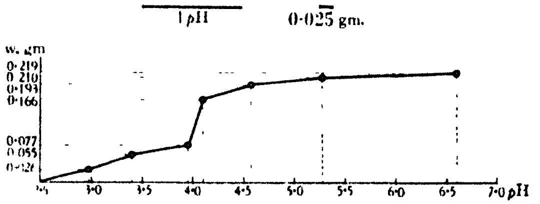

FIG. 50. Buffering of the sap of *Anemone nemorosa*. Abscissae = degrees of *p*H. Ordinates = corresponding degrees of buffering in gm.

The facts gathered during our experiments thus demonstrate a parallelism between the degree of buffering of the saps and the power of the plant to change the reaction of the medium. Whether there exists a causal relation between these two phenomena it is difficult to say, because at present we can carry out but little effective investigation of the properties of the saps. The most we can do is to form a probable conjecture related to the theoretical conception.

VII. CONCLUSIONS.

1. Plants possess in their underground organs the property of changing the reaction of the medium, and this power differs according to the species of plant.

2. Species occurring in the field within the limits of narrow *p*H ranges characteristic of particular plant associations exhibit very clearly both the power of alkalising acidic and of acidifying alkaline liquids.

3. Such species show the same general character of curve, independently of the *p*H in the presence of which the plants were growing in the field. Perhaps it is owing to this property that certain species are strictly attached to certain types of associations.

4. Species of a wide range of occurrence and not attached to specific associations, show curves of a character intermediate between species which are decidedly "alkalising," such as *Corydalis cava,* and those which are extremely "acidifying", such as *Vaccinium myrtillus.*

5. Species taken from a soil of extremely various reactions, while keeping the same general character of the curves, show deviations in alkalisation or acidification.

6. Different reactions of various individuals of the same species on the *p*H of the surrounding medium do not appear to be hereditary. Grown from seeds taken from field conditions of very different *p*H values, plants cultivated on garden beds at the same *p*H show the same curve.

7. Saps expressed from strongly alkalising plants show a very high degree of buffering, specially evident at strongly acid reactions. On the contrary, a ubiquitous species like *Anemone nemorosa,* possesses a feebly buffered sap. It is possible that the degree of buffering of saps is a specific character correlated with the physiological power of the plant to react on the *p*H of the medium.

The present work, begun in the Botanical Institute of the Jagellonian University, was finished in the Silesian Museum in Katowice. Prof. W. Szafer has kindly lent me his apparatus for the measurement of *p*H degrees, and I offer him here my best thanks. I also thank sincerely Prof. Rogoziński for his permission to use the press in his laboratory.

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THE VEGETATION OF REDCLIFF SAND: A CONTRIBUTION TO THE ECOLOGY OF THE HUMBER

By R. D'O. GOOD and W. L. WAUGH

(*With Plates XL and XLI and five Figures in the Text.*)

The great estuary of the Humber, which separates Lincolnshire from Yorkshire, is notorious for the rapidity and extent of the changes taking place in the configuration of its bed and shores. It carries to the sea the drainage of nearly one-fifth of England and an enormous amount of solid matter, apparently reinforced by additional material derived from the south Yorkshire coast, is deposited along its course. The question of the nature and origin of the Humber sand and mud is a controversial one and considerable attention has been paid to it, especially with regard to the part which is played by material derived from the rapid marine erosion of the Holderness cliffs. Fortunately this problem is not directly involved here and it is sufficient to say that while it is frequently possible, by the artificial method of "warping," permanently to reclaim some of the land formed by the settlement of material in the estuary, such products of deposition are normally, if left alone, destined eventually to be destroyed by a reversal of the processes which formed them. Temporary accretions of this kind are a familiar feature of the Humber and it is the botany of one of them that is here described.

Description and history of Redcliff Sand.

The northern shore of the Humber between Hessle and North Ferriby, a few miles west of Hull, is fringed by a long strip of land which may, by courtesy, be termed an island, since at high water it is separated from the mainland by a narrow channel. This island was, when first measured by us in 1929, rather more than a mile long and about 220 yards wide. The whole of it was below the level of extreme high spring tides but nearly all of it was exposed at ordinary high water. Since then it has decreased greatly in width and slightly in length by erosion (Fig. 1).

This island is clearly the result of estuarine deposition at slack water. It has not been altogether easy to unravel the series of events which has led to its present position and form, but, as far as can be stated, the history of it is as follows. A bank of material first began to be deposited in the bed of the estuary towards its southern shore and in a direction south-west from the

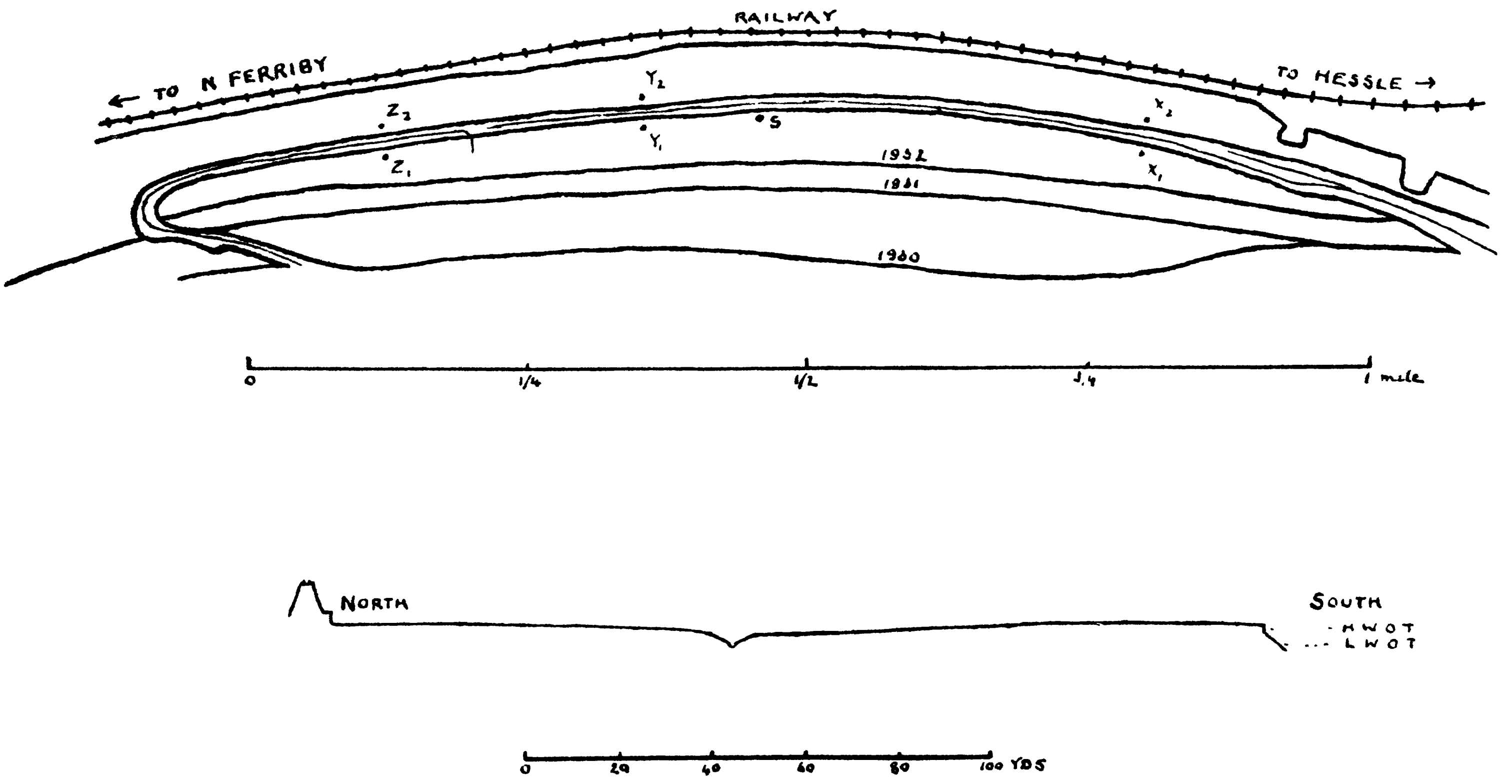

FIG. 1. *Above:* plan of Redcliff Sand (bank) and the adjacent shore (mainland), showing the limits of the former in successive years. S = patch of *Spartina*. X_1—Z_2 = the six points from which soil and water were analysed. *Below:* section of Redcliff Sand and the adjacent shore.

present position of the island. The bank so commenced increased rapidly in height and, at the same time, began to move in a north-easterly direction across the estuary, until after a while it was first visible at low water somewhere about the middle of the estuary. At this period[1] the main navigation channel of the Humber was along or near the north shore, but as the movement of the bank continued this became gradually constricted and a new channel appeared in the wake of the bank near the south shore. After a further period of movement the northern channel became quite closed and the bank began to pile itself up against the north shore. Somewhere about this time the bank attained its maximum area and probably occupied nearly one-third the width of the estuary. As it increased in height it became less and less frequently covered by water at high tide. From this stage the deposition of material largely ceased, although the height continued to augment slowly, and soon the bank began to lose mass by erosion on the southern side. This proceeded rapidly until, in 1929, the size and outline of the island was as described above. Since then it has suffered much further loss. At its maximum the bank was known as Redcliff Sand and this name is retained for its surviving remnant, although for economy of space it is commonly referred to below as the "bank."

In view of the present vegetation of Redcliff Sand it was very desirable to obtain some idea of the time that the various stages in its growth have occupied and of its potentialities as a plant habitat at different times, but this was not easy, as the apposite information did not concern either the land or water geographers and was therefore unrecorded. However, by combining information culled from many sources, it became evident that the building of the bank was no isolated phenomenon but part of a definite cycle of events by which there is a constant rhythmic movement of deposited material in this part of the Humber, from below water-level on the south side of the estuary to above water-level on the north. Associated with this movement is the comparatively sudden shift of the main navigation channel in the opposite direction, namely from north to south. It must not be supposed that this cycle of building, piling up, and erosion is always the same in detail and no particular state is likely to be reproduced exactly in subsequent cycles; but the general rhythm is indubitable. How far the same actual material is used in each cycle we do not know.

We have been unable to obtain any definite records of the length of time involved in this cycle but various isolated facts give an indication. The maximum extent of Redcliff Sand appears to have been about the year 1917 (this is the state shown on the 6 in. ordnance maps of 1928): the beginnings of a new bank are even now visible at low tide somewhere about the centre of the estuary; a rough chart of the year 1901 indicates a condition of affairs very comparable with that to-day: since 1929 erosion has reduced the area of the bank by more than one-half. From such facts and from personal statements made to the authors it may be supposed that the whole cycle lasts about 35 years. More than this it is impossible to say. It is clear that in its early stages Redcliff Sand was entirely uncolonised by plants and that the period during which it has formed a substratum for vascular plants is comparatively short. From the information at our disposal it has probably not exceeded one-third of the whole cycle, or about 12 years.

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[1] This is also the state of affairs at the time of writing.

REDCLIFF SAND AS A PLANT HABITAT.

Redcliff Sand and its vegetation may be studied with interest from many points of view. Here it is considered chiefly as illustrating, in a comparatively simple way, the relation between habitat and vegetation, and the constitution of the latter in terms of the former. In view of this it has been thought more logical to describe the habitat in some detail first and to leave the vegetation account till afterwards.

Topography.

Redcliff Sand to-day is a long narrow strip of sand and mud conforming to the curve of the coast on its north side and having a somewhat parallel erosion escarpment on its southern (riverside) edge. Since it is the remnant of a much larger convex bank which also lay more or less along the shore, its surface slopes slightly towards the mainland and drainage is almost entirely in that direction. It shows also a slight inclination on its longer axis, being highest near its eastern tip and gradually decreasing westward.

The immediately adjacent mainland is a flat strip about 80 yards wide similar to the bank in constitution and bounded rigidly on the north by the embankment of the railway from Hull to Doncaster. The channel separating bank and mainland is about 10 yards wide at high water but at low tide is reduced to two mud slopes and a mere trickle which can be crossed easily on foot.

The southern, river, side of the bank shows, at ordinary high water, a low-stepped cliff. At low tide this is seen to be from 6 to 8 ft. in height, and below this to extend out into the river as a broad slope covered with a scree of water-rounded lumps of mud and clay.

Drainage.

The drainage of the bank is mostly by a series of very remarkable corkscrew runnels leading directly to the separating channel. These runnels are one of the most conspicuous features of the island and are apparently due to certain characteristics of the material making up the bank and to the method of deposition. They are largest at the eastern end, where they may be several feet in depth, and they occur also on the mainland but are here less noticeable. The separating channel itself possesses a watershed rather towards its western end, so that while most of the drainage flows into the Humber round the east end of the bank some goes round the west end. Occasional small runnels can be traced right across the bank, but this is merely because rapid erosion has cut into the longer of those flowing north.

Construction.

The surface of the bank is, when dry, of an ordinary sandy colour, but this gives little clue to its construction, which is best revealed by an inspection of the eroded section. Here it is seen that the bank is built up of a homogeneous deposit of dark muddy clay interspersed at irregular intervals by shallow lenticular beds or bands of yellowish sand. There may be several inches between successive layers or there may be several in the space of a single inch. They vary greatly also in extent and appear for the most part to be local (see Fig. 2).

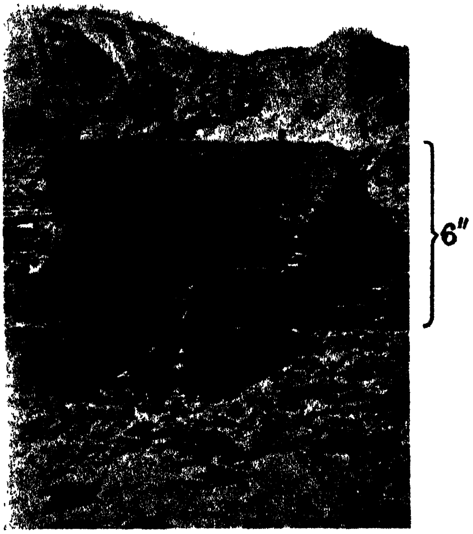


Photo. W. L. W.

FIG. 2. Section of Redcliff Sand on the eroded southern side. Note the dark clay interspersed by shallow beds of sand.

Further examination shows that the mud portion consists about equally of particles of two sizes, larger ones of about 10–15μ and smaller ones about 4μ in diameter. If some of the mud is shaken up in a test-tube and allowed to settle, visible particles are continuing to fall after 10 min., and after 25 min. the liquid above the sediment is still turbid. When this liquid is centrifuged some additional deposit results but the turbidity persists. The black colour of the mud is due to organic matter, chiefly in fine division but occasionally to be seen in fragments of recognisable size.

The sand consists almost entirely of particles 75–100μ in diameter with a very inconsiderable fraction of the smaller particles already noted in the mud. If the sand is shaken up in a test-tube and allowed to settle, the large particles sink in a few seconds and after 10 min. no visible suspension remains although the water is turbid.

Such is the constitution of the purest samples of mud and sand obtainable. Actually, pure mud is present in considerable thicknesses, but pure sand is distributed only in very thin layers.

Surface appearance.

As will be explained later, the surface of the bank varies with circumstances from a very dry to a very wet condition. In the latter it has a surface layer of some 2 in. of liquid grey mud: in the former it frequently dries so completely that the surface splits up into polygonal areas usually some inches in diameter and more or less concave by the lifting of the edges (see Pl. XLI, phot. 5). Such tesselation has, of course, often been observed elsewhere, but here the lamination of the substratum leads to a rather marked effect. If drying continues the actual surface may flake away, but the splitting is usually not very deep vertically and the soil remains damp a very short distance below the surface. This tesselation appears to lead at first to increased drainage from the bank but after a time the corkscrew runnels themselves become dry. It has also been observed that prolonged freedom from tidal immersion usually results in tesselation even if there is copious rain.

Erosion.

A glance at the map (Fig. 1) will show how rapidly erosion is now taking place on the southern face of the bank. The laminated substratum is of considerable importance in relation to this erosion, since the washing out of the sand beds, which is its first effect, hastens the general subsequent disintegration and removal of the more tenacious mud. The very characteristic appearance of minute steps in the erosion face is also due to the same feature (Fig. 2 and Pl. XLI, phot. 7).

Soil analysis.

In order to gain additional information concerning the chemical nature of the deposits six points were chosen (Fig. 1), three on the bank (X_1, Y_1, Z_1) and three on the mainland (X_2, Y_2, Z_2), and samples of the upper 9 in. of the soil from these spots were analysed. The phosphate was precipitated as ammonium phospho-molybdate; the nitrogen was estimated by Kjeldahl's method; the calcium was precipitated as oxalate and weighed as oxide; the potassium was precipitated as perchlorate. The results, expressed as percentages of air-dry soil, were as follows:

	Water and organic matter	Phosphate	Organic nitrogen	Potassium	Total calcium
X_1	18·33	0·0199	0·157	0·515	4·76
X_2	18·86	0·0209	0·200	0·553	4·19
Y_1	17·46	0·0210	0·169	0·670	3·97
Y_2	18·71	0·0208	0·143	0·480	4·43
Z_1	17·24	0·0181	0·145	0·473	3·91
Z_2	18·54	0·0201	0·210	0·600	4·04

It will be noted that there is an appreciable proportion of calcium present and that the phosphate content is very low.

A rough analysis of a general sample of the soil from the six points shows:

Sand	61·4
Al_2O_3 and Fe_2O_3	11·2
P_2O_5	0·02
Organic matter and H_2O	18·0
Calcium	4·0
Potassium	0·55
Total	95·17 %
Undetermined fraction (sulphates, chlorides, nitrates, carbonates, sodium and magnesium)	4·83 %

Hydrogen-ion concentration.

From the same six points as before a series of *p*H determinations were made over the period July-September 1932, inclusive, and using phenol-red as indicator. The results were:

	*p*H					
	X_1	X_2	Y_1	Y_2	Z_1	Z_2
	7·7	7·7	7·6	7·5	7·6	7·6
	—	—	7·7	—	7·7	7·4
	7·6	—	7·7	7·7	7·6	7·7
	7·4	7·3	7·5	7·4	7·4	7·4
	7·7	7·2	7·6	7·4	7·4	7·4
	7·7	7·3	7·7	7·3	7·4	7·4
	—	—	7·6	—	7·4	7·4
	7·7	7·5	7·6	7·3	7·4	7·3
	7·7	7·4	7·5	7·3	7·6	7·4
	7·7	7·7	7·6	7·5	7·5	7·4
	7·4	7·3	7·5	7·3	7·4	7·3
	7·5	7·4	7·7	7·6	7·5	7·4
	—	7·6	7·7	7·7	7·6	7·5
Average	7·6	7·4	7·6	7·5	7·5	7·4

The average values show that all six points are somewhat alkaline and the total range is small, from 7·2 to 7·7. There is also throughout a slightly greater value (i.e. a higher alkalinity) on the bank than on the mainland. This may be associated with the larger proportion of decaying vegetable matter present in the soil of the mainland.

Salinity and other tidal effects.

In physical construction, soil constitution and in alkalinity, the bank as a whole remains very constant and is subject to little variation. In the salinity of the soil, on the other hand, there is marked variation in time and there is little doubt that this is one of the most important factors controlling the vegetation. The soil salinity is naturally bound up with the question of tidal variation in the estuary, and its effect upon the bank, so the two are best treated together.

The Humber is, in the vicinity of Hessle and North Ferriby, markedly tidal and the amount of estuarine water that Redcliff Sand receives, its relative salinity, and the frequency with which the bank may be covered, depend almost entirely on the variation in tidal height, although this may be modified to some extent by such agencies as the wind and the amount of land drainage coming down the contributing rivers. Generally speaking, however, the bank receives saline water in correlation with the tidal variation. The actual tidal values at Redcliff Sand have not been measured owing to the lack of a convenient datum, but a detailed tide-table is available for the Hull docks (King George Dock) about 8 miles east, and for the purposes of this study it may be assumed that except for the modifications already mentioned the same relative variation occurs on the bank.

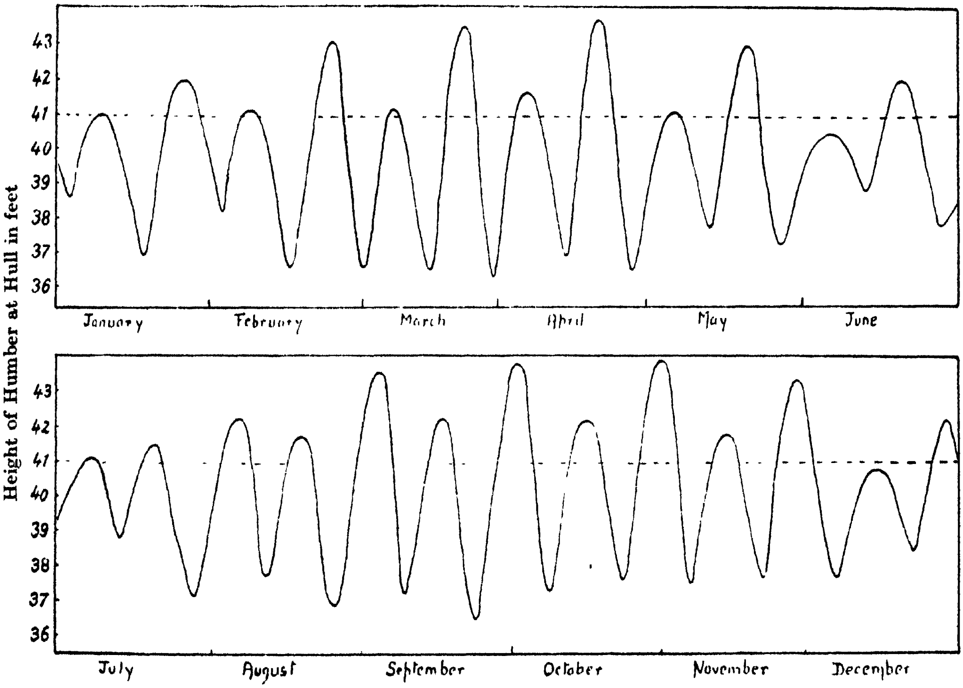


FIG. 3. Graph of the tide values at Hull Docks during the year 1932.

. Fig. 3 is a graph of the high-water tidal values for the year 1932 at Hull and shows well the extent and nature of the variation involved. It may be assumed for present purposes that the possible modifications of drainage and wind tend to cancel themselves out over any lengthy period, such as a year, and therefore that the variation at Redcliff Sand will be relatively much the same as at Hull. By observing certain tides on the bank and noting their value at Hull it appears that, allowing for minor variations, the bank is liable to be covered completely when the Hull figure is about 41 ft. This is the horizontal dotted line on the graph. The number of tides exceeding this figure varies only slightly from year to year and averages a little over 100, a figure representing about 15 per cent. of all tides. These high tides are most plentiful in the months February, March, April and September, October, November and they are fewest in June and July. The longest period occurring between two tides of this value is 25 days, and such periods occur usually at midsummer and midwinter, but the interval is normally shorter and there are generally several high tides in immediate succession. The general rhythm of the tidal variation does not vary much from year to year and this is no doubt of great significance to the vegetation since the same tidal conditions tend to recur at the same stages in vegetative development.

What this variation means to the plants can to some extent be gauged by a study of the value of the total chlorides in the soil water from time to time at the six points already mentioned. The figures obtained (expressed as sodium chloride) are:

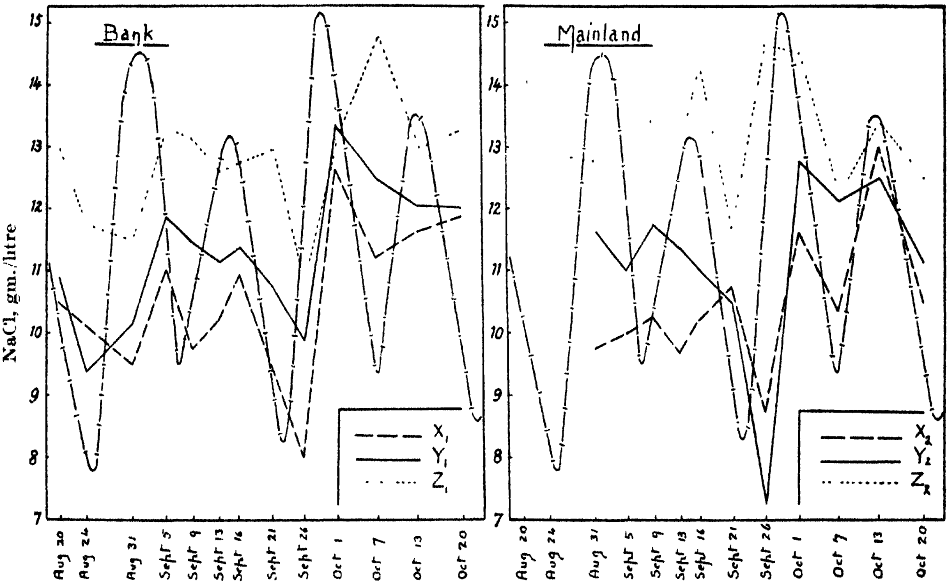
	NaCl gm. per litre					
	X_1	X_2	Y_1	Y_2	Z_1	Z_2
July 7	10·12	9·90	12·71	9·30	9·30	7·90
„ 12	—	—	7·32	—	8·90	7·74
„ 16	9·62	—	7·43	7·10	8·80	7·44
„ 21	8·04	10·00	10·50	12·10	11·20	13·80
Aug. 8	8·59	8·79	8·79	9·33	10·59	11·69
„ 20	10·72	9·94	10·87	11·84	13·13	14·62
„ 24	—	—	9·42	—	11·70	12·84
„ 31	9·62	9·80	10·24	11·65	11·49	12·79
Sept. 5	11·05	10·04	11·96	11·15	13·30	12·60
„ 9	9·80	10·29	11·49	11·75	13·15	13·52
„ 13	10·24	9·72	11·18	11·44	12·48	12·95
„ 16	10·95	10·20	11·44	11·02	12·53	14·35
„ 21	—	10·82	10·52	10·14	12·97	11·62
„ 26	8·06	8·78	9·98	7·28	10·82	14·66
Oct. 1	12·62	11·64	13·42	12·70	13·14	14·50
„ 7	11·15	10·42	12·56	12·24	14·82	12·36
„ 13	11·67	13·10	12·30	12·50	13·10	13·42
„ 20	11·86	10·60	11·90	11·02	13·30	12·56
Average	10·27	10·34	10·66	10·78	12·00	12·35

It will be seen that there is not only considerable variation in absolute value, but a marked difference in time also. Sometimes the figures are twice as much as at others. The average values are also interesting. The figures show that they increase slightly from east to west, that is to say up the estuary, a feature which is presumably due to the more frequent immersion of the west end of the bank. The average salinity is slightly greater on the mainland than on the bank, but the reason for this is not clear, unless it is due to slight differences between the levels of the bank and mainland points.

Estimations of the chloride content of the estuary water off the south side of the bank shows that it varies from 2 gm. per litre at low water, when the effect of the water from land drainage is greatest, to 6 gm. per litre at high water, when the reverse condition obtains. The minimum salinity of the water in the soil of the bank is therefore always more than three times as much as that of the estuary at low water, and always exceeds the value at high water.

The variation in chloride content of the soil water is chiefly of interest in regard to the osmotic relations of the vegetation. The values given indicate that the osmotic value of the water in the upper few inches of the soil is always above 2½ atmospheres and occasionally reaches 5½ atmospheres.

Fig. 4 is a combined graph of tidal value and salinity. The significant general correlation confirms the view that changes in salinity are directly due to tidal differences.



—|—|— represents height of Humber at Hull (from tide tables) *i.e.* x amount of sea-water in the river at Hessle.

FIG. 4. Graphs showing the variation in the salinity of the soil-water on Redcliff Sand and the adjacent mainland.

THE VEGETATION OF REDCLIFF SAND.

(See Plates XL and XLI.)

In describing the vegetation it must be borne in mind that the bank has been under observation for four years and that the plant covering has been developing for a much longer period. Even so there are to-day on the bank only four species in any considerable quantity, although several others have been recorded as occurring more or less sporadically. These four species are therefore described below as the dominant species and the rest are discussed afterwards as occasional species. As far as possible the respective seniority of the species is indicated.

Dominant species.

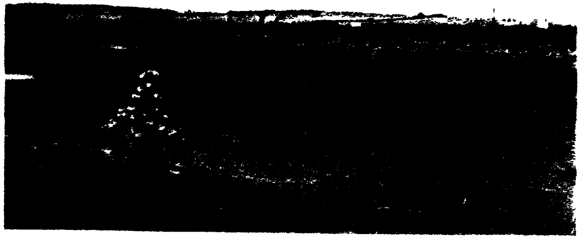
At the present time Redcliff Sand is largely covered with vegetation consisting of the following four species, all of which have been conspicuously plentiful during the time of observation. They are:

Aster Tripolium L., the extraordinary abundance and luxuriance of which is one of the major features of the bank. It occurs all over the area but especially in the eastern part where it forms frequent and dense local communities. It is perennial and grows often to a height of over 6 ft., exhibiting a wide range of variation in form and size. Most of the plants are robust and virgate with stems about an inch in diameter at the base, but spreading or semi-decumbent forms are present. The inflorescence shows all stages between completely radiate and completely discoid heads. White-flowered forms are common. The plants begin to flower in July and are in full bloom till September. They produce ripe fruits abundantly towards the end of that month and dispersal is generally complete by the end of October. The species also multiplies to some extent by short offsets. *Aster* was apparently the last of the four important species to become established on the bank and, as far as our information goes, was not conspicuous before about 1926 or 1927.

Glyceria maritima Mert. and Koch. Although because of its lower habit this species is in general less conspicuous than *Aster*, it is actually more abundant and is the most characteristic constituent of the vegetation. Like the *Aster* it occurs chiefly on the eastern and slightly higher part of the bank but has by now spread nearly all over it. At the east end it forms an almost closed vegetation: on the west it occurs as separate and somewhat scattered circular patches. It flowers freely and is generally in full bloom early in July but the flowering season is not more than three or four weeks. Later in the season it has a second spurt of vegetative growth, spreading over the ground by means of young shoots at the soil level. It fruits well but not conspicuously. This species appears to be the forerunner of Phanerogamous vegetation in such habitats as Redcliff Sand and has been on the bank since about 1920.

Scirpus maritimus L. This species is considerably less abundant than the preceding two but is well established and widespread on the bank. It does not attain a great size, being usually under 2 ft. high and occurs as isolated dense circular patches. It flowers in late July and early August (rather later than on the mainland) and produces copious ripe seed at the end of that month. It is most plentiful in the centre of the bank and rather towards the west end, but scattered patches are widely diffused. The patches increase by means of underground runners or suboles.

Vaucheria dichotoma (Lyngb.) Ag. This alga is particularly abundant over the western half of the bank, especially along the northern side, and also along the edges of the corkscrew runnels. It thus inhabits the lowest and wettest parts of the bank. This fact, and other information given us, indicate

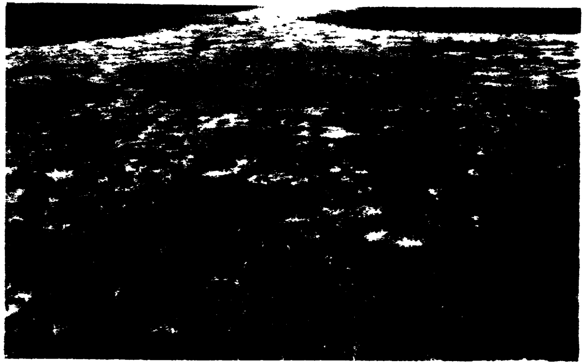


Phot W. L. W.

Phot 1. A patch of *Scirpus maritimus* on Redcliff Sand Single plant of *Aster* in foreground

Phot W. L. W.

Phot. 2. *Aster* plants six feet high on Redcliff Sand *Glyceria maritima* in foreground



Phot W. L. W.

Phot. 3. Surface of Redcliff Sand showing *Vaucheria* in foreground; a clump of *Glyceria* in middle distance.

Phot W. L. W.

Phot 4. Planted patch of *Spartina Townsendi* on Redcliff Sand, showing invasion by *Aster* and *Glyceria*.

that it was the primary coloniser of the area. It has a very definite annual cycle, commencing to grow rapidly about July and increasing till September. After this it gradually diminishes but is always in evidence. At its maximum it forms wide expanses of a dense green carpet a few inches thick which, it is easy to see, catches and holds sediment readily (see Pl. XL, phot. 3). Below the carpet is an evil-smelling black mud which is often exposed over considerable areas by the combined rolling action of winds and tides. Zoospores are produced plentifully in August and September and, at about the same time, it produces what are either oospores or aplanospores. Besides holding sediment it also retains a good deal of water, especially rain, which often stands on it in pools. It extends right to the western extremity of the bank, farther than any of the other three species mentioned.

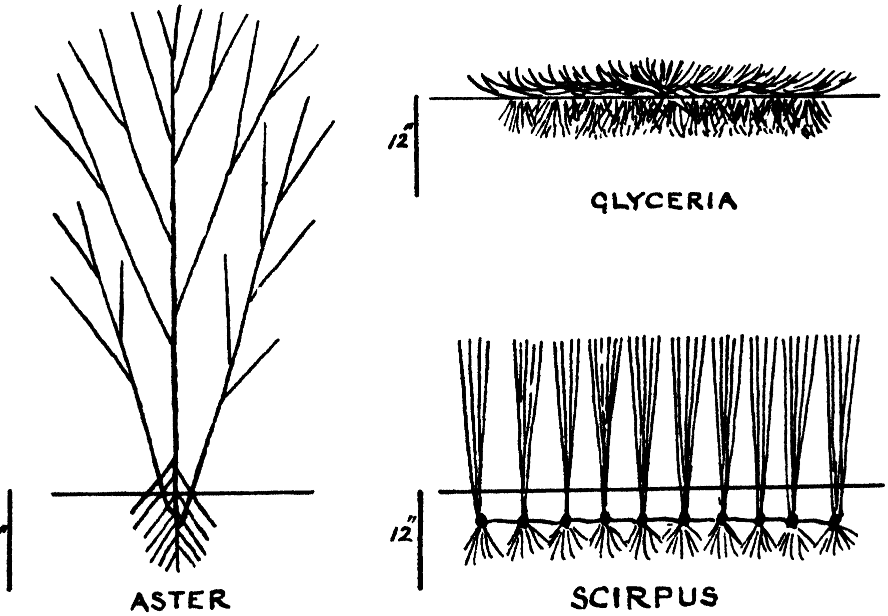


Fig. 5. Diagrammatic representation of the growth forms of the three most important Phanerogams on Redcliff Sand.

Root systems.

A notable feature of the three angiosperms, which are all perennials, is the distinct types of root systems they possess (see Fig. 5). All three are shallow rooted, penetrating only about 9 in. below the surface. *Aster* has a short stout main tap root and comparatively few robust side roots often reinforced by similar adventitious stilt roots from just above ground level. *Glyceria* produces an abundance of fine fibrous roots forming a dense mat below the aerial parts of the plant. *Scirpus* has an intricate system of suboles which run parallel to the surface 3 or 4 in. below it. At intervals these bear small corms, from which the aerial shoots arise and which bear the actual roots. These latter are intermediate in size between those of the other two species.

Anatomy.

Besides these main features of root organisation the three species show a number of interesting minor points in their internal anatomy, and the more outstanding of these may be briefly noted.

Roots. In *Aster* the roots are mostly stout, with a multiple epidermis. There is a wide openwork cortex with many irregular air spaces. In smaller roots this is less developed and is traversed by a few trabeculae only. The xylem is usually tetrarch and secondary thickening soon commences.

In *Glyceria* the roots are very fine. The cortex is very regular and the cells nearly spherical in cross-section so that the intercellular spaces are maximal: the middle layers of cells tend to become trabecular. There is a single layered sclerenchymatous pericycle of about twenty-five cells with several passage cells. The central cylinder has a ring of a very few isolated vessels, alternating with tiny patches of phloem. In the centre is a single large vessel.

In *Scirpus* there is a hypodermis. The cortex is regular and peculiar, consisting of alternating radial rows of rounded and tangentially elongated cells. The narrow phloem is more or less continuous and inside it are three or four isolated vessels. The central pith is sclerenchymatous.

Stems. The general stem anatomy of *Aster* is exceedingly like that of *Helianthus* except that the cortex is wider and has frequent rounded air spaces. The outer layers are green and there is a multiple epidermis. The vascular ring has from sixteen to twenty-five bundles and there is a hollow pith of loosely arranged cells with many air spaces.

In *Glyceria* the stem has an outer green cortex and an inner loose cortex in which the cells tend to become arranged in radial rows with air spaces between. There is a marked fibrous pericycle. The central cylinder has an outer zone of about sixteen bundles contiguous with the pericycle and an inner set of about six larger bundles. The central pith is loose.

The aerial stem of *Scirpus* shows many points of interest. It is triangular in section with a marked hypodermis of very minute sclerenchymatous cells. Near the surface is a zone of rounded air spaces filled with three-dimensional stellate cells and between the spaces are radially elongated cortical cells. Among these cells are two or three concentric rings of small bundles. The pith, which occupies most of the section, is composed of a lattice work of two-dimensional stellate cells, the effect of which is to give a series of vertical ducts. Scattered in this pith are many small bundles.

The corm of *Scirpus* is usually about the size of a hazel nut and has a hypodermis and a slightly stellate cortex. It is mostly made up of a dense central storage tissue, through which are scattered irregularly arranged bundles.

The suboles of *Scirpus* call for special notice. When young they are stout and easily compressed owing to the presence of a broad three-layered cortex. The outer layer of this is of rounded cells: the middle layer has a ring of compressed air spaces: the inner layer is of three-dimensional stellate cells. Minute bundles run irregularly in the cortex. The central cylinder is hard and firm. There is a fibrous pericycle and within this a close compact ground tissue with scattered bundles. As the age of the subole increases the whole of the cortical tissues are shed and the strong central cylinder is left. It appears as a wiry strand connecting up the corms.

The object of these anatomical notes has been to draw attention to certain features in the construction of the species which almost certainly play their parts in fitting the plants for the particular habitat in which they are commonly found. Aerenchyma is of particularly wide occurrence and the distribution of mechanical tissue is also significant. *Scirpus* is the only species with any definite localised storage tissue.

Occasional species.

The following species have also been recorded from Redcliff Sand. They are never conspicuous but scattered and sporadic.

Triglochin maritimum L. First noted in September, 1931, as several plants near the *Spartina* patch (see below) about the middle of the north side of the bank. In 1932 there were at least six plants hereabouts and a few further west. It flowers in July and August and produces plenty of fruit.

Triglochin palustre L. First recorded in July, 1932, in the centre of the bank but later found fairly frequently towards the west end. Flowers in July and August but apparently does not fruit freely.

Glaux maritima L. In September, 1930, only a single plant was seen near the *Spartina*, but several were noted near the west end in 1932. No flowers have been seen on the bank, although the species flowers freely on the mainland.

Atriplex hastata L. Scattered plants of this species have been recorded in the eastern half of the bank throughout the time of observation. It flowers in July and August and produces seed.

Agrostis stolonifera L. Two plants were recorded just east of the centre of the bank in July, 1932. It flowers here and presumably produces fruit.

Enteromorpha intestinalis (L.) Link. A small amount of this alga was recorded at the extreme west end of the bank in July, 1932.

Diatoms and bacteria also occur but have not been studied.

Planted species.

Spartina Townsendi H. & J. Groves. A small patch of this species was planted some years ago on the northern side of the bank about half-way along it. This has maintained itself satisfactorily so far but is now being heavily invaded by *Glyceria* and, to a lesser extent, by *Aster* (see Pl. XL, phot. 4). The plants flower well and presumably produce fruit since there are a few small plants round the original patch, one 50 yards from it. The habitat is not like that in which the plant flourishes in Dorset, and the maintenance of the species here seems precarious. In 1931 most of the inflorescences were infected by two fungi which have been identified for us by the Imperial Mycological Institute as *Epicoccum purpurascens* Ehrenb. and *Claviceps* sp.

CONCLUDING REMARKS.

It was stated on a previous page that Redcliff Sand has been studied chiefly as an illustration of some of the factors which control vegetational development and of the way in which this development proceeds in face of these factors. The more important points may be summarised here.

The constitution of the vegetation as a whole is extremely simple. The great bulk of it, indeed practically all, consists of individuals of three species only (omitting Cryptogams). Five other species are present, but sporadically, and they add nothing to the general plant picture. The three abundant species clearly differ greatly in the degree to which they are in harmony with their environment. *Aster* shows quite an extraordinary development. The individuals are for the most part far above the average size; they show all kinds of minor growth forms: and they flower and fruit copiously. It would probably be difficult to find any other type of habitat in which the plant luxuriates to the same extent, and it seems clear that the conditions of substratum and climate are not only within the range of tolerance of the species as a whole but also within the narrower range of conditions which permits the optimal development of the species.

Glyceria also develops rapidly and successfully on the bank but does not, at any rate in comparison with *Aster*, show very marked luxuriance. It is considerably more copious on the mainland (the reverse is true of *Aster*) and its rate of spread on the island has been in no way prodigious. On the other hand, the specimens on the bank are usually very fine ones. It seems clearly to indicate a different relation between plant and habitat, a state satisfactory enough but by no means absolutely optimal. *Glyceria* appears to find on the bank the conditions necessary for a fully complete and normal development but inadequate to produce exceptional growth.

Scirpus illustrates a further state. It is far less common on the bank than either of the others, although its general appearance makes it fairly conspicuous, and still has a scattered distribution. Besides this, its general growth and stature is, if anything, somewhat below the normal, and it shows no sign of rapid spread. The conditions are obviously not particularly good for this species, although suitable enough to allow of its unobtrusive presence on the bank.

It is known that *Glyceria* preceded the other two on the bank and that *Aster* is of comparatively recent abundance. Unfortunately erosion will have destroyed the habitat before much future observation can be made, but, judging from the mainland, the procedure would probably be the gradual complete supremacy of the *Glyceria* in a closed vegetation and the relative reduction of the other two. Taking this hypothetical future into account, Redcliff Sand illustrates in very simple fashion a major feature of plant succession, the progressive changes in habitat resulting in the passage of conditions from those optimal for one species to those more suited to another.

The occasional species are also of germane interest. Their presence on the bank at all shows that there has been no absence or failure of dispersal from the mainland. Their relative scarcity on the other hand is presumably due to the fact that few have been able to establish themselves and develop largely. The habitat is clearly not so suitable for them as it is for the three species previously discussed. Most of the occasional species have been noted in greater numbers recently and although this may be due to increased observation it probably does represent an actual increase in numbers. This indicates that, as might be expected, the bank is gradually becoming more suitable for them.

In this connection it is worth while referring to the *Spartina*, although it is a planted species. The position appears to be that the plant has maintained itself since it was set but without any appreciable augmentation and that it is now becoming subject to marked invasion and competition. It must also be remembered that it did not originate *in situ* from seed and that quite possibly it would be unable to establish itself by that means.

It should be noticed that competition has played practically no part in the development of the vegetation on the bank. It is noticeable in *Spartina* and of course single individuals of different species often come into collision, but that is all. Redcliff Sand was originally all virgin soil and even now it is by no means covered, so that it can be taken as certain that in no case is the absence of a species from the bank due to competition. This struggle belongs to a later stage in succession.

Four species, *Phragmites communis* Trin., *Digraphis arundinacea* Trin., *Plantago maritima* L. and *Apium graveolens* L. grow on the immediately adjacent mainland but have not been recorded from the bank. Besides these there are in the neighbourhood many others similarly unrecorded on the bank. These latter are not saline species but their absence only serves to emphasise the essential fact that the bank is colonisable only by species with a very particular kind of tolerance. The actual paucity of species upon it seems likely to be due to the two factors of substratum mobility and degree of salinity, since on other parts of the Humber shore where the values of these factors is different such genera as *Salicornia*, *Suaeda*, *Spergularia*, *Obione* and *Cochlearia* are found.

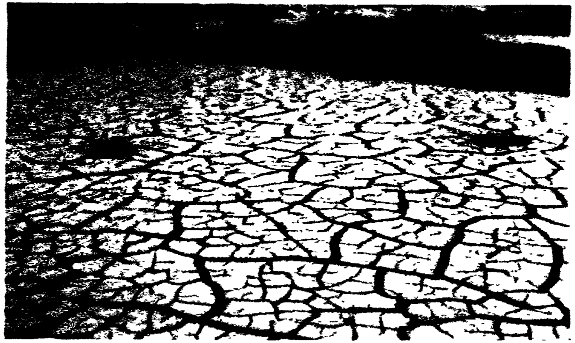
Certainly one of the most important factors of the bank as a plant habitat is the irregularity of the frequency with which it is covered by water and the associated variation in salinity. It would seem that the inhabitants of the bank must have in their constitution some particular means of meeting these difficult conditions and this may be reflected in some of the anatomical points which have been described above.

In this connection the bank also illustrates the importance, in the limitation of vegetation, of minute differences in habitat. This is specially seen in the very marked horizontal limits of *Glyceria* on the north side of the bank. Down to a certain level on the slopes of the separating channel it is normally abundant, but at this level it stops abruptly. As far as can be discovered this line of demarcation is a little below ordinary high water mark. A glance at Fig. 3 however shows that it is difficult to say that any tide value is more "ordinary" than a number of others. If there was a certain tidal value which was very conspicuously more frequent than any other the limitation of *Glyceri* would be more comprehensible. Certainly the mean tides are more numerous, but the curve of frequency is a very gentle one. This being so, it is difficult to escape the conclusion that for some reason or other, not readily apparent, a very slight change in the frequency of immersion and the salinity of the immersing water rigidly controls the presence or absence of *Glyceria* in such habitats as Redcliff Sand.

The last point to be mentioned is the relation of the vegetation to estuarine erosion. Whatever the effects of the plants may be in helping to fix the sediment which is deposited, and some such effect is specially clear in the case of *Vaucheria*, it is equally certain that the vegetation as a whole has no retarding effect whatever upon the erosion of the habitat. Fig. 1 shows how rapid erosion is, and its effects on the plants can be seen at once by a visit to the southern edge of the bank. All over the slope exposed by the receding tide are scattered plants of all three dominant species torn from the bank and still in an almost fresh condition. The actual erosion edge is fringed too with hanging patches of *Glyceria* and *Scirpus* more or less cut away by the disintegration of the soil but held together by their matted roots or suboles. It is in *Aster*, however, that the rapidity of destruction is best observed. Unlike the other two species, these plants are tall and independent and it is no uncommon thing actually to see one of them topple over into the water as the soil in which it grew is washed away (Pl. XLI, Phot. 7).

Taking into account the erosive power of the water and the peculiar construction of the bank, it is difficult to believe that any vegetation could without artificial help withstand the action of erosion. It therefore seems most unlikely that, in situations resembling Redcliff Sand, reclamation by "warping," involving artificial protection from erosion, can ever be satisfactorily replaced by the purely passive effects of vegetational development.

Our gratitude is due to all those who have assisted us, either by furnishing us with information or in other ways and especially to the Humber Conservancy Board for permission to inspect their charts and to Dr B. T. Cromwell for his help with the soil analyses.

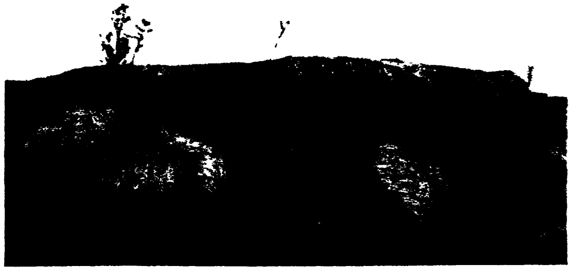


Phot. W. L. W.

Phot. 5. Surface of Redcliff Sand when dry (tesselation). Small plants of *Glyceria* in middle distance *Glyceria* and *Aster* in background.

Phot. W. L. W.

Phot. 6. Dispersal of *Aster* fruits over surface of Redcliff Sand with scattered young *Aster* plants.



Phot. W. L. W.

Phot. 7. Erosion cliff on S. side of Redcliff Sand. Note the plants of *Glyceria*, the *Aster* plant in the act of falling, and the lamination of the cliff.

Phot. W. L. W.

Phot. 8. View of separating channel and mainland (with *Glyceria* and *Aster*) from Redcliff Sand. In foreground is one of the corkscrew drainage runnels; others can be seen in the distance.

POSTSCRIPT, FEBRUARY, 1934.

Since the autumn of 1932, when the foregoing account was written, Redcliff Sand and its vegetation has suffered considerable further change.

Continued erosion has much reduced its area and it is now (February, 1934), nowhere more than 60 yards across. This maximum figure prevails towards the eastern end. The central part has an average width of 50 yards but this gradually diminishes westward, until, for a considerable distance from that extremity, it is reduced to a few yards only. The neck at the west end has been particularly strongly denuded and here the bank is now almost divided into two parts.

The channel between the bank and the mainland has also altered. On its south side the vegetation has encroached so that it is markedly narrower and, besides this, the residual stream remaining at low water has cut a deeper and more defined course.

Except for a few local and small patches, there is now a continuous vegetation of *Glyceria* all over the bank, and, in the east, this has invaded and filled many of the corkscrew drainage runnels. The *Aster* has much decreased and is far less abundant. It is more strictly confined to the minor drainage lines and the plants are of diminished average size. The prominent masses of individuals reaching heights of 5 and 6 ft., formerly present, have quite disappeared.

The planted patch of *Spartina* still flourishes but has not increased, nor does it show any signs of doing so. The colonies of *Scirpus maritimus*, which were mostly on the southern side of the bank, have, for the most part, been washed away.

If the present rate of destruction is maintained it seems probable that the whole of Redcliff Sand will have disappeared within the next three or four years.

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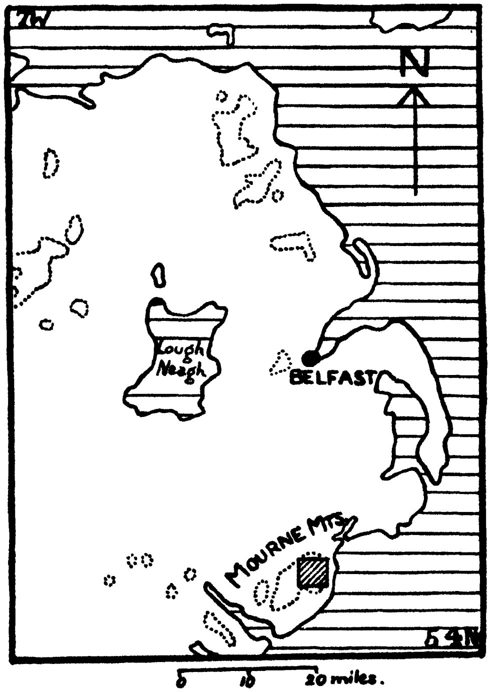
VEGETATION MAP OF THE MOURNE MOUNTAINS, CO. DOWN, IRELAND

By J. I. ARMSTRONG, C. T. INGOLD and K. C. VEAR.

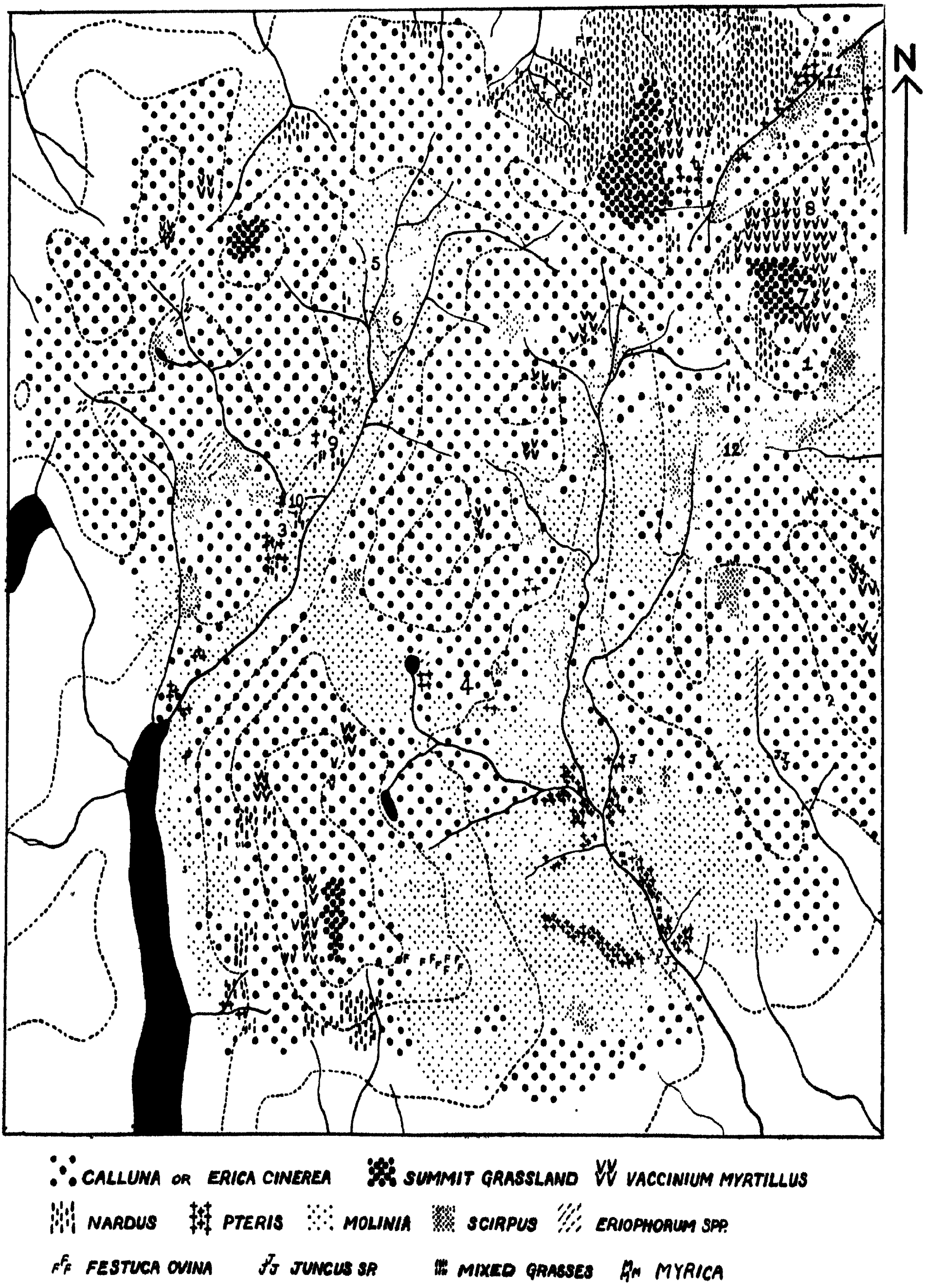
(*With three Maps in the Text.*)

The map was prepared by the authors in the summer of 1932 and shows in a general manner the distribution of the various types of vegetation. In addition to the vegetation map (Map 2) a sketch map (Map 1) is also provided to indicate the extent and geographical position of the area surveyed and a topographical map (Map 3) is included for comparison with the vegetation map and as an index to place-names.

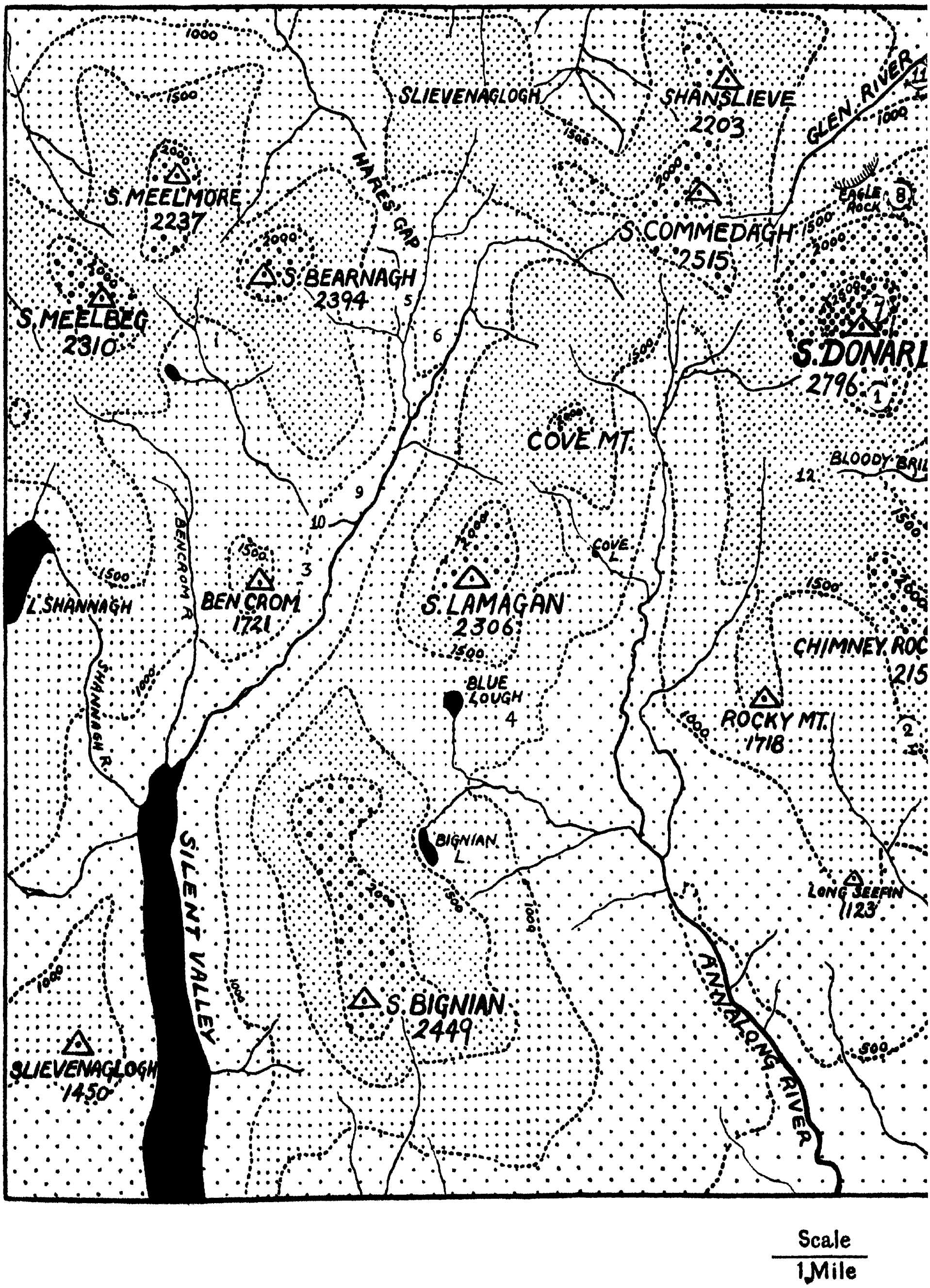


Map 1. Sketch map of north-east Ireland showing location of the area surveyed. Thousand-foot contours are indicated by dotted lines.

A conspicuous feature of the area is that sharp boundaries to communities are rare, except in the case of summit grassland, Ericetum, and Pteridetum. The relatively sharp boundaries of the map do not exist in nature. Further, when the area mapped is noted it is obvious that it was impossible for the



Map 2. Showing distribution of dominant plants.



Map 3. Topographical map and index to place-names. Numbers on summits and contours give height in feet.

authors to enter into great detail of the various communities and consequently no evidence was obtained to show whether the communities were climax except in the case of Eriophoretum, where definite succession was clearly indicated.

The valley vegetation consists in the main of wet moorland dominated by *Molinia caerulea* and *Scirpus caespitosus*, the latter apparently predominating in the wetter regions. Here and there in still wetter parts, for example at the source of the Bloody Bridge River, cotton-grass communities have developed. In damp regions of the Glen River Valley a fairly definite area is dominated by *Myrica gale*. In some well-drained stretches by the river and stream sides, particularly in the Annalong River Valley, communities of bracken occur.

On the hillsides, *Calluna vulgaris* and *Erica cinerea* prevail, passing gradually into the valley vegetation by admixture with *Molinia caerulea* and *Scirpus caespitosus*. On certain sections of the mountain side *Erica cinerea* is definitely the dominant plant. This is particularly noticeable on the north-west slope of Slieve Lamagan at about 1000 ft. *Erica cinerea* also predominates on open morainic areas where large tufts occur separated by stretches of granitic gravel, and it is suggested that in these cases the water content of the soil may be the determining factor. *Vaccinium myrtillus* is frequent on the steep faces of old boulder scree, and a large area on the north and east faces of Slieve Donard is dominated by this plant. *Nardus stricta* becomes an important element of the vegetation on the northern slopes of Slieve Commedagh. It is possible that this feature is associated with the nature of the underlying rock which, in this region, is greywracke shale. This may yield a richer soil than that formed from the granite or granitic gravel which occupies the remainder of the area.

A striking feature of the Mourne Mountains is the development of the summit grassland community on some of the principal peaks (Slieve Donard, S. Commedagh, S. Bearnagh, S. Bignian). In this community, which has been described in detail for Slieve Donard[1], *Rhacomitrium lanuginosum*, *Festuca ovina* and dwarf *Vaccinium myrtillus* compete for dominance. The development of this association is probably due to the absence of peat from the area occupied.

Extensive areas of the hillside have clearly been burnt recently, presumably with the object of ameliorating grazing conditions for sheep, and this burning may possibly have modified the vegetation.

In order to indicate more clearly the constitution of the various communities, typical areas of the more important communities were carefully examined and floristic lists prepared. These are given below and their positions are indicated, and in addition the reference numbers are shown on the vegetation and topographical maps.

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[1] **Armstrong, J. I., Calvert, J.** and **Ingold, C. T.** "The ecology of the Mourne Mountains with special reference to Slieve Donard." *Proc. Roy. Irish Academy*, **39** B, p. 440, 1930.

(1) *Callunetum, high level.* Southern slope of Slieve Donard, 2240 ft.

Calluna vulgaris	d.	Festuca ovina	o.
Erica cinerea	f.	F. vivipara	o.
Carex pilulifera	f.	Carex glauca	r.-o.
Rhacomitrium lanuginosum	f.	Potentilla erecta	v.r.
Agrostis canina	r.-o.	Cladonia rangiferina	v.r.

(2) *Callunetum, low level.* South slope of Chimney Rock Mountain, 1500 ft.

Calluna vulgaris	d.	Vaccinium myrtillus	r.
Erica cinerea	f.	Potentilla erecta	r.
E. tetralix	o.	Eriophorum angustifolium	r.
Molinia caerulea	o.	Cladonia rangiferina	v.r.
Scirpus caespitosus	r.	C. pyxidata	v.r.
Rhacomitrium lanuginosum	r.-o.		

(3) *Ericetum cinereae.* East face of Ben Crom, 1000 ft.

Erica cinerea	d.	Vaccinium myrtillus	r.
Agrostis alba	o.-f.	Polygala vulgaris	v.r.
Calluna vulgaris	o.-f.	Deschampsia flexuosa	v.r.
Galium saxatile	o.	Nardus stricta	v.r.
Potentilla erecta	r.-o.	Blechnum spicant	v.r.
Molinia caerulea	r.	Scirpus caespitosus	v.r.
Pteridium aquilinum	r.	Ulex gallii	v.r.

(4) *Ericetum cinereae.* Bare gravel with tufts of *Erica cinerea* situated on the Blue Lough Moraine, 1000 ft.

Erica cinerea	d.	Agrostis tenuis	v.r.
Calluna vulgaris	f.	Blechnum spicant	v.r.
Scirpus caespitosus	o.-r.	Rhacomitrium lanuginosum	v.r.
Nardus stricta	v.r.	Cladonia pyxidata	v.r.

(5) *Molinietum.* Floor of Silent Valley near head of valley, 1100 ft.

Molinia caerulea	d.	Drosera rotundifolia	r.-o.
Schoenus nigricans	f.	Eriophorum angustifolium	r.
Erica tetralix	f.	Agrostis alba	r.
Sphagnum sp.	f.	Carex glauca	r.
Erica cinerea	o.-f.	Agrostis tenuis	v.r.
Calluna vulgaris	o.-f.	Potentilla erecta	v.r.
Rhacomitrium lanuginosum	o.	Pinguicula vulgaris	v.r.
Scirpus caespitosus	o.	Polygala vulgaris	v.r.

(6) *Scirpetum caespitosae.* Ridge at head of Silent Valley, 1000 ft.

Scirpus caespitosus	d.	Eriophorum angustifolium	o.
Molinia caerulea	f.	Rhacomitrium lanuginosum	o.
Erica cinerea	f.	Cladonia rangiferina	r.
E. tetralix	o.	Sphagnum sp.	r.
Calluna vulgaris	o.	Potentilla erecta	v.r.

(7) *Summit grassland.* Summit of Slieve Donard, 2500 ft.

Festuca ovina	d.	Rhacomitrium lanuginosum	o.-f.
Agrostis canina	f.-co-d.	Carex glauca	o.
Vaccinium myrtillus	f.	C. pilulifera	o.
V. vitis-idaea	f.	Salix herbacea	o.
Empetrum nigrum	f.	Cladonia pyxidata	r.
Galium saxatile	f.		

(8) *Vaccinietum myrtilli.* Eagle Rock in the Glen River Valley, 1500 ft.

Vaccinium myrtillus	d.	Galium saxatile	f.
Deschampsia flexuosa	f.	Sphagnum sp.	o.
Anthoxanthum odoratum	f.	Nardus stricta	r.
Festuca ovina	r.	Blechnum spicant	r.
Agrostis alba	f.		

(9) *Nardetum strictae.* Silent Valley, slope opposite Slieve Lamagan, 500 ft.

Nardus stricta	d.	Galium saxatile	o.
Triodea decumbens	a.	Erica cinerea	o.
Agrostis alba	f.-a.	E. tetralix	o.-r.
Potentilla erecta	f.	Calluna vulgaris	o.
Carex pilulifera	o.-f.	Deschampsia flexuosa	v.r.
C. glauca	o.-f.	Polygala vulgaris	v.r.
Agrostis canina	o.	Rhacomitrium lanuginosum	v.r.
Molinia caerulea	o.	Peltigera canina	r.
Blechnum spicant	o.	Cladonia pyxidata	v.r.

(10) *Pteridetum.* East face of Ben Crom, 1000 or 500 ft.

Pteridium aquilinum	d.	Potentilla erecta	r.
Galium saxatile	a.	Triodea decumbens	r.
Agrostis alba	a.-f.	Polygala vulgaris	v.r.
Blechnum spicant	o.-f.	Vaccinium myrtillus	r.
Molinia caerulea	o.	Cladonia pyxidata	v.r.
Erica cinerea	r.	Peltigera canina	v.r.

(11) *Myricetum.* South side of the Glen River Valley, 1000 ft.

Myrica gale	d.	Eriophorum angustifolium	o.
Molinia caerulea	a.-co-d.	Rhacomitrium lanuginosum	v.r.
Schoenus nigricans	f.	Potentilla erecta	v.r.
Scirpus caespitosus	f.	Erica tetralix	r.
Sphagnum sp.	f.	Polygala vulgaris	v.r.
Erica cinerea	o.	Pinguicula vulgaris	v.r.
Calluna vulgaris	o.	Blechnum spicant	v.r.
Drosera rotundifolia	o.		

(12) *Eriophoretum angustifolii.* Col between Slieve Donard and Chimney Rock Mountain, 1500 ft.

Eriophorum angustifolium	d.	Drosera rotundifolia	o.
Sphagnum sp.	a.	Scirpus caespitosus	r.-o.
Molinia caerulea	f.-a.	Agrostis alba	v.r.
Calluna vulgaris	o.	Potentilla erecta	v.r.
Erica tetralix	o.	Erica cinerea	v.r.

THE VEGETATION OF THE CHILTERN HILLS, WITH SPECIAL REFERENCE TO THE BEECHWOODS AND THEIR SERAL RELATIONSHIPS

By A. S. WATT.

(*With one Figure in the Text.*)

(*Continued from p.* 270.)

CONTENTS.

PAGE

- PART II. THE VEGETATION OF THE PLATEAU 446
  - The scope of the work 446
  - The four seres: A_0, A, B and C 446
  - Distinguishing characters of the four seres 447
    - HABITAT:
      - (1) The varied character of the clay-with-flints and the distribution of the seres upon it 447
      - (2) The soil profile 448
      - (3) Mechanical analyses 451
      - (4) Exchangeable calcium, basicity and hydrogen-ion concentration . . . 451
    - VEGETATION:
      - (1) Floristic composition of the vegetation: frequency and constancy of the species 452
      - (2) Life form 458
      - (3) Structure 461
      - (4) Height growth and density of beech in the beechwoods and the relative vigour of some other species 462
      - (5) The succession 462
  - Description and analysis of the vegetation on the commons and of the four seres . 463
    - The vegetation of the commons 463
      - The grassland facies 464
      - The bracken facies 464
      - The *Calluna* facies 465
      - Woody vegetation 465
      - The relation of trees to grassland 467
      - The relation of woody plants to the *Calluna* facies 467
      - The relation of woody plants to the *Pteridium* facies 467
      - The relation of trees to scrub 468
    - The developing woodland (seres A_0 and A) 468
    - The oakwoods (A_0, A and B) 472
    - The beech associes (A and B + C) 477
    - The beechwoods (A_0, A, B and C) 481
  - Change in the floristic cortège and the constancy and frequency of some species during seral development 489
  - Change in the biological spectra of all species except phanerophytes during the succession in seres A and B 491
  - The effect of beech on the soil 492
  - Discussion of the results. Does beech forest represent the climax community on the Chiltern plateau? 495
  - Some suggestions regarding woodland management 498
  - General comparison between the woody vegetation of the escarpment and that of the plateau 499
  - General comparison with the vegetation of the South Downs 501
  - A note on the relation between the Chiltern beechwoods and the oak-hornbeam woods of Hertfordshire 504
  - Summary of Parts I and II 505
  - Acknowledgments 507
  - References 507

PART II. THE VEGETATION OF THE PLATEAU.

THE SCOPE OF THE WORK.

THE plateau of the Chiltern Hills bears the best and the worst (or nearly the worst) beechwoods in the country. This illustrates at once the wide range of type met with. But to classify these and their intermediates in a linear series of graduated height growth would bring together ecologically unlike, and would separate ecologically related, woods. Comparable growth is found in the floristically rich beechwoods on calcareous loam (a link between the escarpment and the best plateau types), in the beechwoods on undenuded clay-with-flints, on the denuded clay-with-flints commoner further west and on pebbly clay and sand: as also in the poorer types found on brick-earth, exposed flinty eroded slopes, and on the shallow flinty soils of the curved brow of the escarpment. The woody communities described here grow on clay-with-flints and associated brick-earth, but by no means exhaust the types found on the diverse soils derived from these two geological formations.

THE FOUR SERES.

On the basis of floristic, vegetational and edaphic differences four seres are recognised. These are called respectively A_0, A, B and C. The succession in the parallel seres runs as follows: stages not seen, but inferred, are placed in square brackets.

Sere A_0. "Grassland"—scrub—developing woodland (ash-oak)—oakwood—[beech associes]—beechwood.
Sere A. "Grassland"—scrub—developing woodland (ash-oak)—oakwood—beech associes—beechwood.
Sere B. "Grassland"—oakwood—beech associes—beechwood.
Sere C. "Grassland"—[oakwood]—beech associes—beechwood.

"Grassland" is used in a broad sense, including grassland proper, bracken communities, and heather communities—the three facies of the commons—and while differences exist between the commons and between different parts of the same common the reinvestigation necessary to assign different types to their respective seres has not been carried out.

A general shrub colonisation of the commons does not take place and a floristically poor scrub consisting mainly of hawthorn and blackthorn is local, forming small patches without trees or more commonly a fringe to developing woodland. It is probably confined to seres A_0 and A and is not described independently. Ash, oak, beech and locally sycamore invade the scrub and suppress it, forming the developing woodland. The barriers to scrub advance lead to a telescoping of the stages and prevent ash from expressing its natural tendency to form independent woods in advance of the oak. The developing ash-oakwood may be presumed to change into an ash-oakwood or eventually into an oakwood, but most of the existing oakwoods appear to be planted. They constitute an artificial interpolation in the succession and interrupt the continuity between the developing woodland and the equally natural beech associes (formed by the slow advance of the beech in the developing woodland) and while they are regarded as representing the natural oakwood stage, they are not necessarily identical with it. Finally, by suppressing its rivals ash and oak, beech becomes dominant.

Oak invasion of the commons also takes place directly, without the aid of scrub, forming oakwood or, with beech, the beech associes.

The floristically poor scrub upon suppression by thickets of ash and oak leaves no constituents capable of forming a true shrub layer; even in the oakwoods a shrub layer is commonly absent although an open hazel layer may be found, and notably in one wood where the soil has been ridged. This fact is related to the scarcity of coppice, which is rare and probably planted and to the floristic poverty in woody species of coppiced "scrubs." A true shrub layer is quite absent from the beech associes and the beechwoods. Its place is taken in seres A and B by *Rubus fruticosus* (agg.), which, although present on the commons, is not vigorous but develops in all the stages of these seres, varying in vigour with the soil and the tree density, thus demonstrating the greater suitability of the woodland conditions for its growth.

Some species of the field layer are survivors from the open commons: *Agrostis vulgaris* from the grassland itself, *Holcus mollis* chiefly from the shade of *Pteridium*, and *Pteridium* itself. What happens varies with the conditions: in general on the more fertile soils of A_0 and A the change is abrupt from the heliophilous species of grassland to typical woodland herbs. On the poorer types the change is equally well marked but in another direction: the impoverished field layer consists mainly of grasses and sedges. For the woods under investigation seres A_0 and A, with good tree growth, are rich in herbs; C, with poor tree growth, has few species and individuals, mostly of the heathy type; while B is intermediate, comprising the vestiges of A and the rudiments of B.

DISTINGUISHING CHARACTERS OF THE FOUR SERES.

Habitat.

(1) *The varied character of the clay-with-flints and the distribution of the seres upon it.*

The clay-with-flints forms a blanket, of varying origin, thickness and physical properties, overlying the Upper Chalk. The shallower flinty soils on rounded summits (e.g. Sergeant's Wood with chalk at 24 in.) probably consist wholly of the insoluble residue from the Upper Chalk: the deeper deposits are probably the chalk residue and Eocene beds mixed by glacial action. They are essentially loams with scattered flints, which because of denudation (e.g. on valley margins, gentle slopes and in the western Chilterns generally) accumulate at the surface. The thickness of the deposits increases with distance from the escarpment, from about 4–5 ft. to over 50 ft., but to this generalisation there are many exceptions due to varying topography. The pits dug in the beechwoods typical of the seres show a loam not less than 40 in. thick. The soil texture similarly varies: next the escarpment the soil is somewhat coarser, further from the escarpment it is finer in texture. In a general way seres A_0 and A are found next the escarpment, sere C on the finer soils at a distance from it, and B is intermediate in position. But there are many exceptions and the nature of the soil is not uniform throughout each sere, for example the beechwoods of C grow on fine textured soils as well as on acid flinty soils of exposed slopes and of A on shallow, flinty, slightly acid soils as well as on deeper loams with scattered flints. The point is stressed because a more detailed investigation of the whole area must take account of these differences and provide material for a further subdivision and reclassification of the seres.

(2) *The soil profile* (Fig. 1).

Pits dug in beechwoods typical of each of the four seres yield the following data:

A_0 (Ashridge). Most of the wood was cut in 1929–30. The profile was exposed in a marginal remnant where the litter was scattered by wind.

0·5[1]–0 in. Beech-leaf litter, variable in thickness, showing no tendency to form black humus. Locally, where wind-blown litter accumulates, raw humus forms.

0–7 in. Coloured dark by humus; very loose and friable with few flints.

7–36 in. Gradual transition from pale red to rich red soil, becoming stiffer with depth. At 25 in. soil flinty, becoming less flinty below.

Earthworms and mice burrows present. Beech root system diffuse, penetrating at least to 52 in. (1·3 m.).

A (Hailey Wood).

1–0 in. Beech litter variable in thickness: no tendency to form raw humus.

0–7 in. Humus coloured, friable, open-textured soil.

7–20 in. Pale dirty-coloured soil with scattered flints.

20–32 in. Tenacious reddish brown loam, drying to hard prismatic lumps. Scattered flints.

32–52 in. Red-brown with much sand and very flinty.

Earthworms and mice burrows present. Beech root system generally diffuse with a tendency to form the "superficial *plus* sinker" type. Roots penetrate at least to 67 in. (1·7 m.).

B (Keepershill Wood).

2–0 in. Beech litter loose above with a tendency to become laminated below. A thin unmeasurable black coating covers the mineral soil where undisturbed by burrows.

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[1] I.e. half an inch above the soil surface proper.

0–1½ in. Dark humus-coloured soil, very friable.

1½–13 in. Humus colour disappearing quickly, yellowish brown below, compact, tenacious. The surface soil 0–7 in. is very flinty.

13–39 in. Reddish, tenacious, sticky, compact soil with large flints. On drying the soil sets to hard lumps.

Earthworms and mice burrows present. Root system diffuse but bulk of finer roots confined to surface 8 in. Roots penetrate at least to 33 in. (0·8 m.). Oak roots descend to at least 60 in. (1·5 m.).

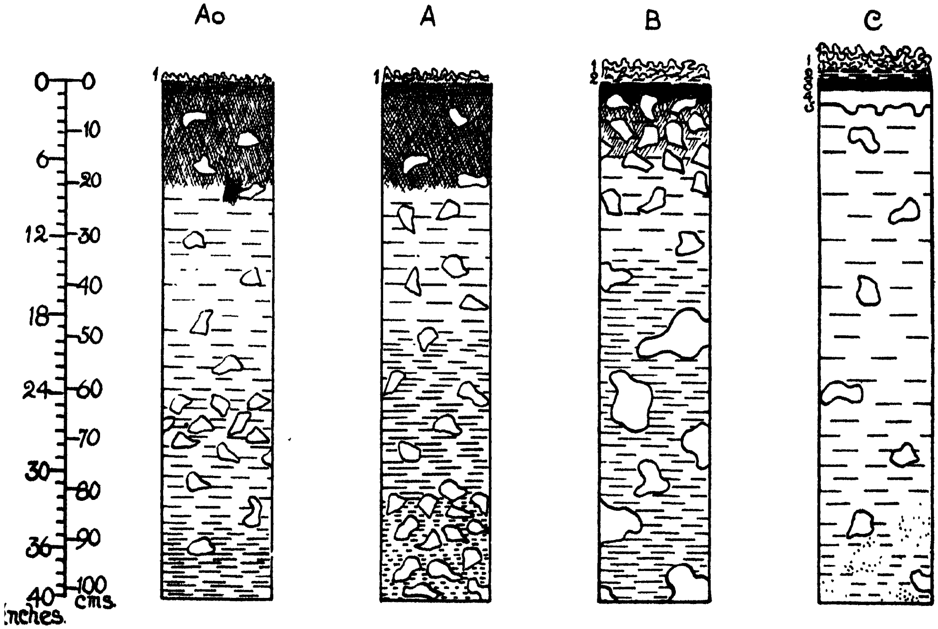

Fig. 1. Profiles of soils in seres A_0, A, B and C. Cross-hatching in the surface soil layer indicates the approximate amount and distribution of humus. The broken lines represent the colour and texture of the soil: the closer the lines the closer the texture and deeper the colour. Dots and short broken lines represent an obvious sand fraction. 1 = leaf litter, 2 = laminated beech litter, incipient in B, 3 = "Trockentorf" and soil horizon A_1, 4 = soil horizon A_2, and 5 = an incipient illuvial (B) soil horizon.

C (Lodge Wood).

3–1 in. Loose beech litter.

1–½ in. Laminated litter, leaves above, whole, disintegrating below.

½–¼ in. Black peaty humus.

¼–0 in. Black peaty humus with some mineral soil.

0–¼ in. Black humus-coloured soil.

¼–1¼ in. Grey, almost white, layer, variable in depth. Immediately below is a thin but distinct undulating illuvial horizon.

1–16 in. Pale yellow compact soil, powdery when dry.

16–31 in. Stiffer, mottled grey-yellow-red tenacious soil.
31–40 in. Mottled grey-red. Small sandy pockets.

Compactness of the soil increases with depth. Flints few but scattered throughout. No earthworm burrows in the soil, although a few earthworms are found in the surface peat. Abandoned mice burrows form a reticulum of surface canals.

Root system diffuse, penetrating at least to 34 in. (0·8 m.). There is no concentration of larger roots near the surface but certainly the bulk of the finer rootlets lie in the raw humus overlying the mineral soil.

In each soil type there is a colour gradation from the surface downward to a depth of about 36 in., where all the soils are varying shades of rich red, but the steepness of the gradient rises from A_0 to C. Determinations of the sesquioxide content however in the surface 6 in., at 12–15 in., 27–30 in. and at 33–36 in. reveal a more or less uniform distribution throughout. The soil of C, with glei formation below, is distinctly podsolised at the surface.

Two important facts stand out from these descriptions: the first concerns the texture of the surface soil, the second the distribution of the organic matter. In seres A_0, A and B the soils sink under the foot: they contain many earthworms and are penetrated by numerous burrows made by higher animals, mice and moles. The soil of C is compact, and as firm as a pavement under the foot: earthworms are scarce and confined to the surface "Torf," and there is no mouse activity. These facts are connected with the amount and distribution of the organic matter both above and in the soil. Data concerning the distribution of humus in the surface 6 in. of soil are given on p. 493: the following show the weight in grams of litter collected in April from 1 sq. ft. in each of the seres A, B and C.

	Sere A	Sere B	Sere C
Beech leaves	30·5	56	50
Beech raw humus	0	Thin coating not collectable	455
Oak leaves	1	Less than 0·5 gm.	3·5
Twigs of beech, oak bramble, beech cupules, etc.	37	27·5	19

The two sets of data together show that in seres A_0 and A the organic matter becomes thoroughly incorporated in the surface mineral soil, the gradient from the surface downwards being very gentle; in B the surface litter is more abundant, there is a distinct tendency to form raw humus and the gradient in the soil is steep. In C the accumulation continues; the litter is about the same weight but the thin cover of black humus in B has increased in thickness forming a well-marked layer, and humus staining of the soil reaches about ¼ in. only. The series marks the change from soils of the brown-earth type to a podsol.

The brief notes on the root system of the beech show that although various tendencies are evident there is no general restriction of the root system as a whole to the surface-soil layers.

(3) *Mechanical analysis of fine soil in the surface* 6 *in.*

It should be noted that the fraction passing the 1 mm. sieve was analysed and not the 2 mm. fraction as recommended in the Revised Official Method (*Agr. Progress*, **5**, 1928).

	A_0	A	B	C
Coarse sand	6·66	2·41	9·91	1·16
Fine sand	37·36	36·84	27·00	31·04
Silt	36·25	38·41	32·25	49·12
Clay	7·55	6·77	18·25	8·40
Moisture in air dry soil	2·51	3·50	2·23	1·41
Carbonates	Nil	Nil	Nil	Nil
Loss by solution in peroxide HCl treatment	3·45	3·71	2·92	2·71
Difference (organic matter removed by hydrogen peroxide and errors of experiment)	6·22	8·36	7·44	6·16
Loss on ignition (determined independently)	7·41	7·41	6·12	5·75

It is clear from the data respecting coarse sand, fine sand and silt that A_0, A and C form a series: B is a truncated soil with a protective flint layer at the surface. All the soils however are characterised by a high content in fine sand and silt and a relatively low clay content except in B with two to three times as much. The high silt content confers clay-like properties on the soils but makes them more amenable to treatment with humus than with calcium carbonate. Calcium carbonate is in fact absent from the surface soil as well as from all levels down to 36 in. The data from these forest soils may be contrasted with those given by Temple (**7**) for clay-with-flints under arable conditions or pasture. Practically all contain free calcium carbonate and more in the surface layers than below, "evidence of the applications of chalk, during the early days of last century" ((**7**), pp. 52 and 53).

(4) *Exchangeable calcium.*

"Exchangeable calcium usually ranges about 0·4 to 0·5 per cent." ((**7**), p. 52). The data from the forest soils are very much lower and form a series, A_0 with 0·142 per cent., A with 0·058 per cent., B with 0·002 per cent. and C with 0·001 per cent.

Basicity. To obtain a comparison of the total amounts of bases in the respective soils, soil extracts in N HNO_3 obtained by De Sigmond's method (**6**) give the following values: A_0, 28; A, 18; B, 22·8; and C, 11·6. They fall into De Sigmond's first two groups with very low values.

Hydrogen-ion concentration. All the soils contain manganese, but C has much less than A_0, A and B. Consequently the *p*H data (**8**) obtained by the quinhydrone method are too high (**2**). Using Kuhn's colorimetric method, I get the following values for samples of the surface 6 in. of soil: A_0, 5·2; A, 4·7; B, 4·6; C, 4·1. In the soil profile of A_0 the *p*H of samples taken at successive 3 in. levels shows a rise from 4·7 at the surface, to a maximum of 5·8 at 6–9 in., and thereafter a fall to 4·7 at 12–15 in., remaining practically constant below. In A from 4·3 at the surface the *p*H rises gradually to 6·0 at 30–33 in., remaining constant at lower levels. In B, the range of *p*H is very small; from

4·6 at the surface it falls to a minimum of 4·2 at 9–12 in., thereafter generally rising to 4·6 again at 27–30 in., and remaining constant down to 39 in. The data for C were obtained by the quinhydrone method and show low values throughout with a range from 3·85 in the lower layer of raw humus to a maximum of 4·65 at 37–40 in.

These data throw some light on the vegetational phenomena, but they are inadequate to afford anything like full explanation. All the soils are well drained and essentially dry, except in small patches and in hollows where water may stand throughout the summer; but in virtue of their high content in the finer fractions they are retentive of moisture. Judging from the growth of the trees and the presence and vigour of some herbs believed to be exacting in their demands for soil minerals, seres A_0 and A are fertile and C is very infertile with B intermediate. Yet while the data reveal a gradient in *p*H, in exchangeable calcium and in basicity the soils are all highly acid with no calcium carbonate at all and a low percentage of exchangeable calcium. Furthermore, writing of the clay-with-flints under cultivation, Temple says, "the phosphoric acid content is on the low side, and potash, while sufficient for most plant requirements, is not so high that it cannot be supplemented with beneficial results." High acidity, as Vageler (**10**) points out in reference to tropical soils, does not imply low fertility. But the analysis does not appear exhaustive enough to enable us fully to understand the combination of exceptional vigour in some species with soils whose analysis would imply infertility—unless, indeed, our ideas about what plants can or cannot do requires considerable revision. The anomaly is rendered still more striking by the presence in all seres of the nitratophilous ***Epilobium angustifolium*** and ***Rubus idaeus***: it is clear that despite the absence of $CaCO_3$ and the high acidity, nitrification can take place.

Vegetation.

(1) *Floristic composition of the vegetation: frequency and constancy of the species.*

Since the total number of examples, the areas covered, the seral status of the examples, and their number and degree of development in each sere vary so much, comparisons cannot be pushed too far. This applies in particular to A_0 where each stage is represented by not more than two examples and the beechwood by a single example only, with the additional drawback of an immature subsidiary vegetation. Absence of a species, therefore, is not always a safe guide in drawing conclusions respecting the soil and the relationships between the seres. C is represented by beechwoods and a beech associes which is really mixed B and C, rendering comparison with the earlier stages of the other seres impossible or inferential only. A, on the other hand, is quite well represented: its characterisation is therefore the more complete.

These inequalities must in part account for the differences in the total number of species found in the separate seres: but part is due to variation in soil fertility. The numbers in the respective seres A_0, A, B and C are: phanerophytes, 21, 39, 25, 11; herbs, grasses, 2 *Rubi* and *Tamus*, 65, 103, 76, 52; bryophytes, 20, 33, 21, 18. The gradation in numbers from A to C may be accepted as an expression of decreasing soil fertility, since it is repeated in the figures for the beechwoods of these seres (where the number of examples—10, 7, 5—makes the results of comparison more reliable); and more especially since the diminution is largely due to the progressive elimination of more exacting species from the less fertile habitats of B and C.

The floristic affinities are indicated by the number of species common to pairs of seres, expressed as a percentage of the total found in the two taken together.

	Phanerophytes	Herbs, etc.	Bryophytes
A + B	60	57	49
B + C	39	62	48
A + C	22	38	38
A_0 + A	46	50	56
A_0 + B	53	41	54
A_0 + C	39	31	31

The large number of phanerophytes in A disturbs the relations: it gives us the anomalous result that the relationship between A and A_0 is apparently less close than between A_0 and B. Among herbs in cognate seres 50 per cent. or more of the species are found in common: about 40 per cent. in seres at one remove and 30 per cent. at two. The bryophytes show the same general feature. The species common to A_0 and C are, with one exception, found in all four seres: they comprise nine phanerophytes, twenty-seven herbs, etc., and nine bryophytes.

A consideration of these and of the lists as a whole brings out several important features. In soils so very acid it is surprising to meet with species commonly regarded as characteristic of alkaline or only slightly acid soils. Yet, though present, their distribution among the seres is restricted. Between A_0 and A on the one hand and B and C on the other, there is a fairly sharp cleavage, for A_0 and A are essentially characterised by a large number of the more exacting species (*Acer campestre*, *Euonymus europaeus*, *Cornus sanguinea*, *Ligustrum vulgare*, *Solanum dulcamara*; *Adoxa moschatellina*, *Ajuga reptans*, *Asperula odorata*, *Arctium minus*, *Brachypodium silvaticum*, *Bromus asper*, *Festuca gigantea*, *Galium aparine*, *Hordeum silvaticum*, *Lactuca muralis*, *Poa nemoralis*, *Sanicula europaea*, *Stachys silvatica*; *Eurhynchium piliferum*, *E. striatum*, *Fissidens taxifolius*, *Mnium undulatum*) while the flora of B and C is made up of more tolerant species like *Agrostis vulgaris*, *Deschampsia caespitosa*, *Luzula pilosa* and *Hypnum cupressiforme*, found in all seres, together with characteristic acidiphilous species, *Calluna vulgaris*, *Carex pallescens*, *Deschampsia flexuosa*, *Hypericum humifusum*, *Sieglingia decumbens*, *Stachys betonica*, *Hypnum schreberi* and *Leucobryum glaucum*. This segregation of some acidiphilous species in B and C contrasts with the occurrence in all four seres of others (*Conopodium denudatum, Galium saxatile, Holcus mollis, Dicranella heteromalla*) while *Scilla non-scripta, Digitalis purpurea* (A_0, A, B) *Stellaria holostea* (A, B), *Hypericum pulchrum, Rumex acetosella* (A, B, C), *Stellaria uliginosa* (A_0, A, C) and *Diplophyllum albicans* (A and C) bridge the gap between. Their exclusion from some seres may be accidental; others, like *Scilla*, may be excluded because of unsuitable soil texture. Further, the association of exacting and acidiphilous species is not more striking than the presence in all four seres of the nitratophilous *Rubus idaeus, Epilobium angustifolium* and *Urtica dioica*, which though mostly found in gaps nevertheless reveal the potentialities of the habitat.

The flora of B is intermediate between A and C: it includes an overflow from A and the well-springs of C. It has therefore less character than either.

The effects of local soil variation are eliminated, and more clear-cut distinctions between the different seres are brought out by considering only the species significant in each (pp. 455–457). Significant species here include those with constancy 4 and 5 and/or average frequency of 2·1 and over together with certain species with lower values considered as having significance in differentiating the seres. These last are assigned to their respective seres, partly on the basis of the values shown and partly on my general experience of their habits. This course is rendered necessary because most of the species in the beechwoods are included on a high constancy value, and constancy values are not obtainable from the few examples of sere A_0.

The significant species are listed in four groups: group (1) contains species with high values in all four seres; groups (2), (3) and (4), the differential phanerophytes, herbs, etc., and bryophytes respectively, arranged in order from A_0 to C. Species marked "l." are local, but in assigning a species to its sere or seres consideration has been given to the cause of its limited distribution; if due to local soil variation the species is regarded as an outlier of its proper sere; if excluded from the wood as a whole by shade, its presence in gaps is regarded as a useful pointer in establishing affinities, and on that ground the species is held to merit inclusion among significant species. This holds good especially for the beechwoods of C. Where the number of examples of any community is less than four the letter notation of frequency is used.

The differences already noted when all the species are taken into account become sharper when the significant species only are examined. The lists reveal the greater floristic wealth of A_0 and A (70 and 106 species) compared with B and C (54 and 47). The exacting trees, herbs and bryophytes are confined to A_0 and A and account for the numerical superiority of these seres, but acidiphilous species are represented by *Scilla* (A_0, A), *Stellaria holostea* (A) with *Digitalis* (A, B) bridging the two groups; they increase in relative importance in B and C, *Hypericum humifusum, Stachys betonica, Sieglingia* (B), *Hypericum pulchrum, Anthoxanthum odoratum, Hypnum schreberi* (B, C), *Calluna, Deschampsia flexuosa, Rumex acetosella, Carex pallescens, C. pilulifera,* *Species with constancy 4 or 5 and/or average frequency of 2·1 and over, and differential species in seres A_0, A, B and C.*

			Sere A_0			Sere A				Sere B			Sere C
			Developing woodland	Oakwood	Beechwood	Developing woodland	Oakwood	Beech associes	Beechwood	Oakwood	Beech associes (B+C)	Beechwood	Beechwood
Seres in which species is significant	Life form§	Number of examples ...	2	2	1	4	6	8	10	7	1	7	5
			F.*	F.	F.	C.†, A.F.‡	C., A.F.	C., A.F.	C., A.F.	C., A.F.	F.	C., A.F.	C., A.F.
Group (1). Species significant in all four seres.													
A_0, A, B, C	P.	Fagus silvatica	o.-l a.	o.	d.	5, 2·0	5, 2·3	5, 4·0	5, 5·0	5, 2·3	o.-f.-l.d.	5, 5·0	5, 5·0
A_0, A, B, C	P.	Quercus robur	f.-a.	f.-d	o.	5, 3·6	5, 4·8	5, 4·2	5, 2·5	5, 4·4	a.-d.	5, 2·6	5, 2·2
A_0, A, B, C	P.	Lonicera periclymenum	o.-l f.	o.-f.-l.a.	—	5, 2·8	5, 2·8	5, 2·6	5, 1·7	5, 2·9	f.	5, 1·7	2, m.
A_0, A, B, C	H.r.	Oxalis acetosella	f.-l.a.	o.-f.-l.d.	o.m.	5, 2·3	5, 2·6	5, 2·5	5, 2·9	5, 2·0	o.-l.f.	5, 2·9	4, 2·2
A_0, A, B, C	H.s. (G.r.)	Epilobium angustifolium	l.f.	o.-l.a.	l.	3, 2·5 l.	1, 2·0	2, 2·3 l.	3, 1·8 l.	1, 2·0	—	4, 1·8 l.	3, 1·8 l.
A_0, A, B, C	H.s.	Rubus fruticosus (agg.)	o.-l.a.	o.-f.-l d.	o.-m l.f.	5, 3·3	5, 4·2	5, 3·5	5, 4·6	5, 4·8	o.-f.-l.a.	5, 4·7	5, 2·2
A_0, A, B, C	H.c.	Deschampsia caespitosa	o.-l.d.	o.-f.-l.d.	—	4, 2·2	4, 2·0	2, 2·3	5, 2·5	3, 2·0	l.	5, 2·4	5, 2·0
A_0, A, B, C	H.c.	Holcus lanatus	o.	o.	—	4, 1·8	3, 1·7	2, 1·5	3, 1·4	3, 1·7	l f.	4, 2·0	4, 2·0
A_0, A, B, C	H.c.	Juncus communis	l.a	o.-f	—	—	1, 2·5 l.	2, 1·3 l.	3, 1·2 l.	—	—	4, 1·2 l.	4, 1·8 l.
A_0, A, B, C	G.r.	Holcus mollis	o.l.	o.-l f.	—	4, 2·0	5, 2·2	4, 2·2	3, 2·0	5, 2·6	o.-l.a.	4, 2·7	5, 1·9
A_0, A, B, C	G.r.	Pteridium aquilinum	o.-f.-l.d.	f.-l.d.	m l.f.	5, 2·5	5, 2·8	5, 2·3	4, 1·6	5, 3·0	o.-f.-d.	5, 2·2	5, 1·8
A_0, A, B, C		Dicranella heteromalla	o.-f.	o.-l.a	o.	4, 1·7	4, 1·8	4, 2·3	4, 1·8	4, 2·0	o.	5, 2·2	5, 2·2
		Hypnum cupressiforme	o.-l.f	o.-l.f.	o.	2, 2·0	3, 2·0	5, 2·2	4, 2·0	3, 2·0	o.	4, 2·0	5, 2·0
		Mnium hornum	o.-f.	o.-l f.	o.	5, 2·4	5, 2·1	4, 2·0	4, 2·0	3, 2·0	o.-l.f.	5, 2·1	5, 3·0
		Thuidium tamariscinum	o.-l.f.	o.-l.f.	—	4, 3·0	3, 2·3	4, 2·3	3, 1·8	3, 2·0	l.	3, 2·0	4, 2·1
Group (2). Woody species significant in three seres or less.													
A_0	P.	Euonymus europaeus	o.	r.	—	—	—	—	—	—	—	—	—
A_0	P.	Rosa tomentosa	—	o.	—	—	—	—	—	—	—	—	—
A_0	P.	Ribes rubrum	—	o.-l a.	—	—	2, 1·0	—	1, 1·0	—	—	—	—
A_0, A	P.	Acer campestre	o.	o.	—	2, 1·5	1, 1·0	—	1, 1·0 m	—	—	—	—
A_0, A	P.	Fraxinus excelsior	f.-a.-l.d.	f.	o.	5, 3·3	5, 2·1	3, 1·5	5, 2·2	3, 1·5	l.	2, 1·5	—
A_0, A	P.	Prunus spinosa	o.-l.a.	—	—	5, 2·3	2, 1·5	1, 1·0 l	—	1, 1·0 l.	o.	—	—
A_0, A	P.	Sambucus nigra	f.-l d.	o.-f	o.-l.f.	5, 2·0	3, 2·0	2, 2·0	3, 1·7	1, 2·0	—	2, 2·0	—
A_0, A, B	P.	Acer pseudoplatanus	o.-l d.	o.-l d.	—	4, 2·5	2, 2·3	1, 1·0	2, 2·3	3, 2·3	—	2, 2·0	—
A_0, A, B	P.	Corylus avellana	o.-l f.	o.-f.	—	5, 2·0	5, 2·5	2, 2·0	2, 1·3	4, 2·0	l.	2, 1·0	—
A_0, A, B	P.	Crataegus monogyna	r.-l.a.	r.	—	5, 3·1	5, 2·1	4, 2·0	2, 1·8	4, 2·0	o.	4, 1·4	1, 1·0
A	P.	Cornus sanguinea	—	—	—	1, 2·0	2, 2·0	—	—	—	—	—	—
A	P.	Ligustrum vulgare	—	—	—	2, 2·0	1, 3·0 l.	—	—	—	—	—	—
A	P.	Solanum dulcamara	—	—	—	1, 1·0 l.	2, 1·0 l.	—	—	—	—	—	—
A	G.b.	Tamus communis	—	—	—	1, 2·0	1, 1·0 l.	—	—	—	—	—	—
A	P.	Rosa arvensis	r.	r.	—	4, 2·0	4, 1·8	3, 2·0	5, 1·6	3, 2·0	o.	1, 1·0	—
A	P.	Viburnum opulus	o.	o.	—	1, 2·0	5, 2·0	3, 1·5	2, 1·0 l.	—	—	1, 1·0 l.	—
A, B	P.	Hedera helix	—	o.	—	3, 2·8	3, 2·2	4, 2·2	3, 1·8	3, 2·5	o.-l.f.	3, 2·0	1, l.
A, B	P.	Prunus avium	—	r.-o.	—	5, 2·0	2, 1·5	4, 2·0	5, 1·9	2, 2·0	o.	5, 1·6	3, 1·0
A, B, C	P.	Ilex aquifolium	—	r.-o.	—	4, 2·1	4, 1·8	5, 1·8	5, 2·1	5, 1·8	f.-l.a.	5, 2·1	5, 2·2
B, C	P.	Juniperus communis	—	—	—	—	—	—	—	—	o.-l.f.	—	—
B	P.	Quercus sessiliflora	—	—	—	—	1, 2·0	—	—	2, 3·5	—	1, 2·0	—
B	P.	Q. robur × sessiliflora	—	—	—	—	2, 2·0	1, 1·0	—	3, 2·2	l.	2, 2·0	—
C	P.	Salix aurita	—	—	—	—	—	—	—	—	—	—	1, 1·0

§ P. = phanerophyte; Ch. = chamaephyte; H.r. = rosulate, H.c. = caespitose, H.s. = scapose hemicryptophyte; G.b. bulbous, G.r = rhizomatous, G.rad. = radicigemmate geophyte; T. = therophyte.

* F. = frequency. † C. = constancy. ‡ A.F. = average frequency.

Seres in which species is significant	Life-form		Sere A_0			Sere A				Sere B			Sere C
			Developing woodland	Oak-wood	Beech-wood	Developing woodland	Oak-wood	Beech associes	Beech-wood	Oak-wood	Beech-associes (B+C)	Beech-wood	Beech-wood
		Number of examples ...	2	2	1	4	6	8	10	7	1	7	5
			F.*	F.	F.	C.†, A.F.‡	C., A.F.	C., A.F.	C., A.F.	C., A.F.	F	C.. A.F.	C., A.F.
			Group (3). Herbs, etc., significant in three seres or less.										
A_0	H.s.	Heracleum sphondylium	—	r.	—	—	—	—	—	—	—	—	—
A_0	T.	Myosotis arvensis	o.	—	—	—	—	—	—	—	—	—	—
A_0	G.r.	Paris quadrifolia	—	l.	—	—	—	—	—	—	—	—	—
A_0	H.s.	Filipendula ulmaria	—	l.	—	—	—	—	—	—	—	—	—
A_0, A	H.s.	Ajuga reptans	o.	o.-f.	—	4, 2·0	4. 1·8	4. 2·0	2. 2·0	—	—	—	—
A_0, A	H.s.	Arctium minus	r.-o.	—	—	2, 2·0	1, 1·0	—	2, 1·7	—	—	—	—
A_0, A	T.	Arenaria trinervia	o.-l.f.	o.-l.f.	—	4. 2·0	2, 2·0	2, 2·0	2. 1·5	—	o.	2, 1·0 l.	—
A_0, A	G.r.	Asperula odorata	o.l.	o.-f.	—	4, 3·3	3, 2·5	3, 2·3	5, 2·7	1, 1·0 l.	l.	—	—
A_0, A	H.c.	Brachypodium silvaticum	o.	o.	—	4, 1·3	1, 1·0 l.	1, 1·0	1, 1·5	—	—	—	—
A_0, A	H.c.	Bromus asper	—	r.	—	2, 2·0	2, 2·0	1, 2·0	3, 1·6	—	—	—	—
A_0, A	G.r.	Circaea lutetiana	o.-l.f.	f	—	4. 2·5	5. 1·9	3, 1·5 l.	5. 2·1	—	1. 1·0 l.	3, 1·0 l.	3, 1·0 l.
A_0, A	H.s.	Cirsium palustre	—	o.	—	2, 1·5	1, 2·0	—	—	—	—	—	—
A_0, A	H.s.	Epilobium montanum	o.	o.-l.f.	—	3, 1·5	2, 2·0	2, 2·0	4, 2·0	—	—	2. 1·0 l.	1, 1·0 l.
A_0, A	H.r.	Fragaria vesca	o.-f.	o.	—	4, 2·0	2, 1·5	1. 1·0 l.	3. 2·0	2. 1·5	—	—	—
A_0, A	T.	Galium aparine	o.	o.-l.f.	—	3, 2·0	2, 1·5	1. 3·0	2. 2·3	—	—	—	—
A_0, A	H.s.	Geum urbanum	o.-f.	o.-f.	—	4, 1·8	2, 2·0	2, 2·0	5, 1·6	—	l.	—	—
A_0, A	Ch.	Lamium galeobdolon	o.-f.-l.a.	o.-f.-l.a.	—	2, 4·0 l.	5. 2·7	4, 2·6	4. 2·1	—	—	—	—
A_0, A	H.r.	Lastrea dilatata	o.	o.	o.	2, 2·0	3, 1·7	3, 1·7	1, 1·0	—	—	1, 1·0	1, 2·0 l.
A_0, A	Ch.	Lysimachia nemorum	o.	o.	o.m.	2, 2·0	3, 1·7	3, 1·3	2, 1·8	1, 1·0 l.	—	3, 1·0 l.	1, 1·0 l.
A_0, A	H.s.	Mercurialis perennis	f.-l.d.	f.-l.d.	l.d.	2, 2·0	3, 2·2	1, 1·0 l.	3, 1·3 l.	1, 3·0 l.	—	—	—
A_0, A	Ch.	Nepeta glechoma	f.-a.-l.d.	o.-f.-l.a.	—	5, 2·5	4, 2·5	1, 4·0	1, 2·0	—	—	—	—
A_0, A	H.c.	Poa trivialis	o.-f.	o.	—	4, 1·7	3. 1·3	2, 1·5	1. 2·0	1. 1·0 l.	o.	3, 2·0	2. 1·0 l.
A_0, A	H.r.	Primula vulgaris	l.f.	o.	—	3, 2·0	3, 1·7	2. 2·0	1, 1·5	1. 2·0	—	—	—
A_0, A	H.s.	Ranunculus auricomus	r.	—	—	—	—	—	1. 1·0	—	—	—	—
A_0, A	H.r.	Sanicula europaea	l.	o.-f.	—	4, 2·5	4, 2·4	2, 2·0	3, 1·8 l.	—	—	—	—
A_0, A	G.b.	Scilla non-scripta	f.-l.a.	o.-f.-l.d.	—	5, 1·8	4, 3·3	2. 2·5	4, 2·2 l.	1, 2·0 l.	o.	1, 1·0 l.	—
A_0, A	H.s.	Scrophularia nodosa	o.	o.	—	—	2, 1·5	—	2, 2·0	1, 1·0 l.	—	1, 1·0	—
A_0, A	H.s.	Senecio jacobaea	—	o.	—	—	1, 2·0	—	—	—	—	—	—
A_0, A	H.s.	Urtica dioica	o.-l.a.	o.-l.f.-l.a.	l.f.	3, 1·5	1. 2·0	—	3, 1·8	—	l.	—	2. 1·0 l.
A_0, A	Ch.	Veronica chamaedrys	o.	o.-l.	—	4, 2·0	2, 1·5	—	1, 1·5	1, 1·0 l.	—	—	—
A_0, A	Ch.	V. montana	o.	o.	—	2, 3·0	2. 1·5	3. 2·0	4, 1·9	—	—	1, 1·0 l.	—
A_0, A	H.r.	Viola silvatica	o.	o.-f.	o.	5. 1·9	5, 1·9	3, 1·8	5, 2·2	3, 2·0	o.	3, 1·8	1, 1·0 l.
A_0, A, B	H.r.	Athyrium filix-foemina	l.	o.-l.f.	o.	2, 2·0	3, 2·0	2. 2·0	3, 1·6	—	—	3, 1·5	1, 2·0
A_0, A, B	H.c.	Carex silvatica	o.	o.	—	3, 2·0	5, 1·8	3, 1·5	5, 2·1	1, 2·0	—	4, 1·5 l.	1, 2·0
A_0, A, B	H.r.	Dryopteris filix-mas	o.-l.f.	o.-l.f.	o.	3. 2·3	4. 2·0	4, 1·8	5. 2·1	—	—	4, 1·8	1. 1·0
A_0, A, B	H.s.	Rubus idaeus	o.	o.	—	2, 2·5	2. 2·3	2, 1·5 l.	4, 1·7 l.	1. 1·0 l.	l.	4. 1·6 l.	2. 1·5 l.
A	H.s.	Adoxa moschatellina	—	—	—	1. 2·0	—	—	1, 1·0 l.	—	—	—	—
A	H.c.	Agropyrum caninum	—	—	—	1, 2·0	—	—	1, 1·0 l.	—	—	—	—
A	G.r.	Anemone nemorosa	—	—	—	—	2, 2·0	2. 2·0	2, 2·3	—	—	—	—
A	H.s.	Angelica silvestris	—	—	—	2, 1·0 l.	—	1, 1·0 l.	—	—	—	—	—
A	G.b.	Arum maculatum	—	—	—	3. 2·0	1. 1·0 l.	—	2. 1·7	—	—	—	—
A	H.c.	Carex strigosa	—	—	—	—	—	—	1, 1·0	—	—	—	—
A	Ch.	Euphorbia amygdaloides	—	—	—	—	2, 2·0	1. 2·0	4. 1·7	2. 1·5	l.	—	—
A	H.c.	Festuca gigantea	r.	—	—	4, 1·7	—	2. 1·5	3. 2·0	—	—	—	—
A	T.	Geranium robertianum	—	l.	—	4, 1·7	1, 2·0	2, 2·0	5. 2·2	—	—	1, 1·0 l.	—
A	G.r.	Helleborine latifolia	—	r.	—	2, 2·0	—	—	4. 1·8	1, 1·0	—	—	—

A	H.c.	Hordeum silvaticum	—	—	—	2, 2·0	—	—	2, 2·0	—	—	—	—
A	H.s.	Lactuca muralis	—	—	—	—	—	—	1, 1·0	—	—	—	—
A	G.r.	Listera ovata	—	—	—	2, 1·0 l.	1, 1·0	—	—	—	—	—	—
A	G.r.	Melica uniflora	—	—	—	2, 2·0	1, 1·0 l.	2, 2·2	4, 2·0	—	o.	—	1, +
A	G.r.	Phegopteris polypodioides	—	—	—	—	1, 1·0 l.	—	—	—	—	—	—
A	H.c.	Poa nemoralis	—	—	—	2, 2·0	—	—	2, 1·0	—	—	—	—
A	G.r.	Polygonatum multiflorum	—	—	—	—	1, 2·0	—	—	—	—	—	—
A	H.s.	Ranunculus ficaria	—	—	—	2, +	—	—	2, 4 0 l.	—	—	—	—
A	H.s.	R. repens	l.	.	—	4, 1·7	1, 1·0 l.	2, 2·0	—	1, 2·0	—	1, 1·0 l.	2, 1·0 l
A	H.s.	Stachys silvatica	—	—	—	3, 1·5	2, 2·0	—	2, 2·0	—	—	—	—
A	Ch.	Stellaria holostea	—	—	—	3, 2·0	2, 1·8	2, 2 0	4, 1·7	1, 1·0 l.	l.	1, 1·0 l.	—
A, B	H.r.	Blechnum spicant	—	—	—	—	1, 1·0	3, 1 5	1, –	—	1, 2·0	1, 2 0	—
A, B	H.s.	Digitalis purpurea	—	r.	—	4, 2·0	3, 1·7	2, 2 0	1, 2·0	1, 2·0	o.	5, 2·2 l.	—
A, B	H.c.	Milium effusum	—	o.	—	2, 1·0 l.	3, 1·7	2, 2·3	5, 2·1	—	o.	5, 1·9	3, 1·3
A, B	T.	Senecio silvaticu	—	—	—	—	1, 2·0	—	—	—	—	1, 1·0	—
A, B, C	H.c.	Agrostis vulgaris	o -l f.	—	—	2, 2·0	2, 2 0	4, 2 0	1, 1 0 l.	5, 1·7	o -f.-l.a.	5, 1·9	5, 2·0
A, B. C	H.c.	Carex remota	—	—	—	2, 2·0	1, 1 0 l.	2, 2 0	5, 1·8	—	2, 1·0 l.	4, 2·0	4, 2·2
A, B, C	H.c.	Luzula pilosa	—	r l.	—	—	4, 2·0	5, 1·8	5, 1·9	1, 2·0	o.	5, 2·0	5, 2·2
A, B, C	G.rad	Monotropa hypopitys	—	—	—	—	—	1, 1·0	1, 1·0	—	—	1, 2 0	2, 2·0
B	H.s.	Hypericum humifusum	—	—	—	—	—	—	—	—	—	1, 2·0 l.	—
B	H.c.	Sieglingia decumbens	—	—	—	—	—	—	—	—	—	1, 1·0	—
B	H.s.	Stachys betonica	—	—	—	—	—	—	—	1, 1·0 l.	—	—	—
B, C	H.c.	Anthoxanthum odoratum	—	—	—	2, 2 0	1, 2·0	—	—	1, 2·5	o.-l.f.	2, 1·5	4, 2·0
B, C	H.c.	Festuca ovina	—	—	—	—	—	—	—	—	o	1, 3 0 l.	3, 2·0
B, C	H.s.	Hypericum pulchrum	—	—	—	—	—	1, 2·0	—	3, 1·7	o.	3, 1 7	4, 1 5
C	H.c.	Agrostis alba	—	—	—	2, +	2, 1·5	2, 1·0 l.	1, 1·0 l.	—	—	1, 2·0	1, 3·0 l.
C	Ch.	Calluna vulgaris	—	—	—	—	—	—	—	2, 1·0 l.	o	1, 2·0 l.	5, 1·4 l.
C	H.c.	Carex pallescens	—	—	—	—	—	—	—	—	—	—	1, 1·0 l.
C	H.c.	C. pilulifera	—	—	—	—	1, 2·0	—	—	1, 2·0	—	—	1, 3·0 l.
C	Ch.	Deschampsia flexuosa	—	—	—	—	—	—	—	2, 1·5	l.f.	—	1, 3·0 l.
C	T.	Poa annua	—	—	—	—	—	1, +	1, 1·5	—	—	2, 1·0	4, 1·2 l.
C	Ch -H.s.- G.rad.	Rumex acetosella	—	—	—	—	—	—	1, 1·0 l.	—	l.	2, 1·5 l.	1, 3·0 l.

Group (4). Bryophytes significant in three seres or less.

A_0, A	Catharinea undulata	.-l.d.	o.-l.f.	o.	4, 2 3	4, 2·0	5, 1·9	3, 1·8	2, 2·0	o.	2, 2·0	1, 1·0 l.
A_0, A	Eurhynchium striatum	o.-f.	o.	—	3, 2·7	3, 2 2	2, 1·5	1, 2·0	2, 2·0	—	—	—
A_0, A	Fissidens taxifolius	o.	o.	+	2, 2 0	2, 2·3	1, +	2, +	2, 2·0	—	—	—
A_0, A	Mnium undulatum	f.	o.-l.f.	—	4, 2·5	2, 1·5	1, 2·0	1, +	—	—	—	—
A	Calypogeia trichomanis	—	—	—	—	2, 2 0	1, 1·0 l.	—	—	—	—	—
A	Eurhynchium piliferum	l.f.	—	—	2, 3·0	1, 2·0	—	—	—	—	—	—
A_0, A, B	Brachythecium rutabulum	o.-f.	o.	—	2, 2 0	2, 2·0	—	3, 2·0	1, 2·0	—	3, 1·8	—
A_0, A, B	Eurhynchium praelongum	f.	f.-l.a.	o.	4, 3·3	5, 2·5	4, 2·0	4, 2·0	3, 3·0	—	2, 2·0	2, 2·0
A, B, C	E. myosuroides	o.	—	—	2, 2 0	—	3, 2·0	4, 2·0	+	1, 1·0 l.	4, 2·0	5, 2·5
A, B, C	Polytrichum formosum	—	—	—	4, 1·7	2, 1·0 l.	4, 2·1	5, 2·0	5, 2·3	o.-f.-l.a.	5, 2·4	5, 3·3
B, C	Dicranum scoparium	o.	—	—	—	2, 2·0	2, 1·7	2, 2·0	2, 2·0	o.	4, 2·1	5, 3·0
B, C	Hypnum schreberi	—	—	—	—	—	—	—	1, 2·0	—	—	1, 1·5
B	Webera nutans	—	—	—	—	—	—	—	—	—	1, 1·0 l.	—
C	Cephalozia bicuspidata	—	—	—	—	—	—	—	—	—	—	2, +
C	Diplophyllum albicans	—	—	—	—	—	1, +	—	—	—	—	4, 2·0
C	Frullania tamarisci	—	—	—	—	—	—	—	—	—	—	1, +
C	Hylocomium loreum	—	—	—	2, 1·0 l.	—	—	1, 1·0 l.	1, 2·0	—	1, 1·0 l.	4, 1·3
C	Lepidozia reptans	—	—	—	—	1, 1·0 l.	—	—	—	—	—	4, 2·0
C	Leucobryum glaucum	—	—	—	—	—	—	—	—	—	1, 1·0 l.	2, 1·5

* F. = frequency. † C = constancy. ‡ A.F. = average frequency.

Leucobryum glaucum (C), while *Holcus mollis* and *Dicranella heteromalla* are significant in all four seres.

The significant occurrence of exacting species distinguishes A_0 and A from B and C. To separate the seres within these two groups reliance may be placed on presence or absence and constancy and average frequency values. In connection with these values it may be noted that the species with really high frequency values are those common to the four seres and include the species dominant in the respective seral stages and in the respective layers within these.

While the scarcity of material forbids conclusions being drawn from the absence of species from A_0, presence in A_0 and absence from A, where the examples are numerous and widespread, may be considered significant. Thus *Euonymus*, *Rosa tomentosa*, *Heracleum sphondylium*, *Myosotis arvensis*, *Paris quadrifolia*, *Filipendula ulmaria*, are all present in A_0 and absent from A. If we turn to frequency values comparison is again difficult, but the differences in *Rubus fruticosus* (agg.) and *Mercurialis perennis* are outstanding. *Rubus* is never more than locally dominant in A_0 and is more often occasional only, while even in the developing woodlands and under the dense shade in the beech associes of A it has a consistently high frequency. Mercury, on the other hand, is the characteristic plant of A_0, where it has a high average frequency, while in A it has relatively low values both of average frequency and constancy.

To distinguish B from C one may utilise part of the overflow from A: *Corylus*, *Crataegus*, *Rubus idaeus*, *Prunus avium*, *Hedera*, *Carex silvatica*, *Dryopteris filix-mas*, *Milium effusum*, all have significant values in B and are either absent from, or have low values in C. Or reference may be made to *Rubus fruticosus* and *Oxalis acetosella*, both of which have high values in B, but high constancy and low frequency values only in C. The acidiphilous flora in the gaps of the beechwoods of C is also characteristic.

(2) *Life form.*

The biological spectra reveal features of special interest. They have been calculated from (1) all species, (2) "significant" species only, and (3) species with high constancy and average frequency values only; but although the actual percentages vary the essential features stand out the same in the results of all three methods of calculation. Spectra for all species and for the significant species are given on p. 459, worked out with and without phanerophytes. The distribution of the life forms of species exclusive to the different seres taken singly or together is shown in Table I.

In the spectra of all species there is fair uniformity in all seres among the same life-form classes or subclasses except the scapose and caespitose hemicryptophytes: and in the relation between these two lies the main point of difference. In A_0, hemicryptophytes with leafy flowering stems easily outnumber the caespitose forms; in A there is an approach to equality, with the

Biological spectra of all species in seres A_0, A, B and C.

The actual number of species belonging to each life form is given in parentheses after the percentage number.

Sere	P.	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	G.rad.	T.	Total
				(1) Including phanerophytes.						
A_0	24 (21)	9 (8)	12·5 (11)	24 (21)	14 (12)	8 (7)	2·5 (2)	0	6 (5)	100 (87)
A	27 (39)	7·5 (11)	9 (13)	20 (29)	17·25 (25)	9 (13)	2·5 (4)	1·5 (2)	6·25 (9)	100 (145)
B	24 (25)	10·5 (11)	9·5 (10)	17·5 (18)	20 (21)	7·75 (8)	2 (2)	2 (2)	6·75 (7)	100 (104)
C	16·5 (11)	9 (6)	9 (6)	15·5 (10)	32 (21)	9 (6)	1·5 (1)	3 (2)	4·5 (3)	100 (66)
				(2) Without phanerophytes.						
A_0	—	12	16·5	32	18·5	10·5	3	0	7·5	100
A	—	10·5	12·25	27	23·5	12·25	4	2	8·5	100
B	—	14	12·5	23	26·5	10	2·5	2·5	9·0	100
C	—	11	11	18	38	11	2	3·5	3·5	100

Biological spectra of significant species in seres A_0, A, B and C.

Sere	P.	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	G.rad.	T.	Total
				(1) Including phanerophytes.						
A_0	22·5 (13)	8·5 (5)	14 (8)	26 (15)	12 (7)	10·5 (6)	1·5 (1)	0	5 (3)	100 (58)
A	20 (18)	8 (7)	10 (9)	22·5 (20)	18 (16)	12·5 (11)	3·5 (3)	1 (1)	4·5 (4)	100 (89)
B	31 (12)	0	10·5 (4)	18 (7)	28 (11)	7·5 (3)	0	2·5 (1)	2·5 (1)	100 (39)
C	19·5 (6)	9·5 (3)	3·25 (1)	13 (4)	35·5 (11)	9·5 (3)	0	6·5 (2)	3·25 (1)	100 (31)
				(2) Without phanerophytes.						
A_0	—	11	17·5	33·5	15·5	13·5	2·5	0	6·5	100
A	—	10	12·5	28	22·5	15·5	4·5	1·5	5·5	100
B	—	0	15	26	41	11	0	3·5	3·5	100
C	—	12	4	16	44	12	0	8	4	100

Table I. *Distribution of the life forms of species significant in A_0, A, B and C.*

Seres in which significant	P.	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	G.rad.	T.	Total
A_0, A, B, C	3	—	1	2	3	3	—	—	—	12
A_0, A, B	3	—	2	1	1	—	—	—	—	7
A, B, C	1	—	—	—	3	—	—	1	—	5
A_0, A	4	5	5	10	3	2	1	—	2	32
A, B	2	—	1	1	1	—	—	—	1	6
B, C	1	—	—	1	2	—	—	—	—	4
A_0	3	—	—	2	—	1	—	—	1	7
A	5	2	—	6	5	6	2	—	1	27
B	2	—	—	2	1	—	—	—	—	5
C	1	3	—	1	3	—	—	1	1	10
Total	25	10	9	26	22	12	3	2	6	115 (112 species)

scapose forms slightly more numerous; in B this position is reversed; while in C the caespitose hemicryptophytes easily preponderate.

The same feature is accentuated in the spectra of significant species. But other features also emerge. In B there are no chamaephytes; in B and C no bulbous geophytes, and there is a general reduction in rosette hemicryptophytes from A_0 to C. Further, from Table I it is clear that C has no rosette hemicryptophytes and B and C have no rhizome geophytes peculiar to them, for the representatives of these life forms in the relevant spectra are common to all four seres. The commanding position of scapose hemicryptophytes in A_0 and A is due to species confined to these two seres. At the same time the other life forms, chamaephytes, rosette hemicryptophytes and rhizome geophytes are relatively well represented.

The phanerophytes show a gradual reduction in number from A to C: *Euonymus, Ribes rubrum* and *Rosa tomentosa* are confined to A_0, *Juniperus communis* to mixed B and C and *Salix aurita* to C. The limitation of *Quercus sessiliflora* and the hybrid to B is probably due to planting. The absence of chamaephytes from B illustrates the intermediate position of this sere: it falls between A_0 and A with the herbaceous *Lamium galeobdolon, Lysimachia nemorum, Nepeta glechoma, Veronica chamaedrys, V. montana* (A_0, A), *Euphorbia amygdaloides, Stellaria holostea* (A) and of C with woody *Calluna,* tufted *Deschampsia flexuosa* and herbaceous *Rumex acetosella.* Among rosette hemicryptophytes *Oxalis* is common to all seres, *Fragaria vesca, Lastrea dilatata, Primula vulgaris, Sanicula europaea, Viola silvatica* are limited to A_0 and A, *Athyrium filix-foemina, Dryopteris filix-mas* to A_0, A and B and *Blechnum spicant* to A and B. Two scapose hemicryptophytes (*Epilobium angustifolium, Rubus fruticosus*) are common, while the following are confined to the seres named after them: *Heracleum sphondylium, Spiraea ulmaria* (A_0), *Adoxa, Angelica, Lactuca, Ranunculus ficaria, R. repens, Stachys silvatica* (A); *Ajuga, Arctium, Cirsium palustre, Epilobium montanum, Geum, Mercurialis, Ranunculus auricomus, Scrophularia, Senecio jacobaea, Urtica* (A_0, A), *Hypericum humifusum, Stachys betonica* (B); *Rubus idaeus* (A_0, A, B), *Digitalis purpurea* (A, B), *Hypericum pulchrum* (B, C); *Rumex acetosella* (C). Similarly with the caespitose hemicryptophytes: *Deschampsia caespitosa, Holcus lanatus, Juncus communis* (all seres), none is peculiar to A_0, *Brachypodium silvaticum, Bromus asper, Poa trivialis* (A_0, A); *Agropyrum caninum, Carex strigosa, Festuca gigantea, Hordeum europaeum, Poa nemoralis* (A); *Carex silvatica* (A_0, A, B), *Milium effusum* (A, B), *Sieglingia decumbens* (B), *Agrostis vulgaris, Carex remota, Luzula pilosa* (A, B, C), *Festuca ovina, Anthoxanthum odoratum* (B, C), and *Carex pallescens, C. pilulifera, Agrostis alba* (C). The rhizome geophytes common to all and the only representatives of this class in B and C are *Holcus mollis, Epilobium angustifolium,* and *Pteridium,* the rest are confined to A_0 and A, *Paris* (A_0), *Asperula, Circaea* (A_0, A), *Anemone, Helleborine, Listera ovata, Melica uniflora, Phegopteris polypodioides, Polygonatum multiflorum* (A). *Scilla,* among bulbous geophytes is significant in A_0 and A, and *Tamus* and *Arum* in A. Among root-bud geophytes *Monotropa* occurs in the beechwoods of A, B and C and it is unlikely that its absence from A_0 is of any significance, while *Rumex acetosella* is confined to C. Finally the annuals, *Myosotis arvensis* (A_0), *Arenaria trinervia, Galium aparine* (A_0, A), *Geranium robertianum* (A), *Senecio silvaticus* (A, B) and *Poa annua* (C) complete the list.

Although no detailed studies have been made, the predominance of tall-growing scapose hemicryptophytes and rhizome geophytes may account in part for the smaller number of species in A_0, in which however the early-flowering *Scilla* forms a colourful spring aspect. The failure of such vernal species as *Anemone* and *Ranunculus ficaria* to form a definite spring aspect, except locally, in A, is to be sought, as is also the low frequency of scapose hemicryptophytes, in a consideration of the structure of the communities.

(3) *Structure.*

Neither in oakwoods nor in beechwoods is there a true shrub layer except locally in oakwoods (A) where *Corylus* has probably been planted; in A_0 the oakwoods show the rudiments of a shrub layer, with *Corylus*, *Sambucus* and *Ribes rubrum* the chief constituents. Its place in A and B is taken by a layer of *Rubus fruticosus*, which varies in height and density according to the sere and the shade. In A_0 oakwoods, it is locally dominant only without showing clear indications of ability to assume general dominance, whilst in the beechwood it is marginal and perhaps potentially dominant; in C (beechwoods) a *Rubus* layer is absent or local only.

In A_0 variation in the composition of the field layer is largely determined by the shade cast by the trees, and such diverse forms as *Oxalis*, *Scilla*, *Mercurialis*, *Pteridium* are each locally dominant. In the beechwood one-half of the ground is bare: the rest is occupied by *Mercurialis* with *Rubus* marginal only. Thus the field layer is free to develop in the absence of *Rubus*, and in the mature oakwood it forms a continuous layer. Bryophytes are scarce and become locally dominant (*Catharinea undulata*) only where higher plants are excluded by shade. Thus the oakwoods of A_0 consist essentially of a tree layer, a rudimentary shrub layer and a rich herbaceous field layer, whilst in the immature beechwood the shrub layer is replaced by a potential *Rubus* layer.

In A, continuity of the field layer is the exception, but *Oxalis* is locally dominant under the heavier shade of even-aged relatively younger beeches which prevents a vigorous growth of *Rubus*, and in the planted oakwoods immaturity of the subsidiary vegetation is indicated by locally dominant *Pteridium*, *Scilla* and *Holcus mollis*. But typically it consists of scattered rather miserable individuals, surviving but never robust, under the shade of a layer of *Rubus*. This explains the low average frequency shown by most herbs and grasses, and the failure of the bryophytes to form a continuous layer. If for any cause *Rubus* is sparsely represented and the beech-leaf litter is removed, as for example on the exposed wind-swept margins of beechwoods, *Holcus mollis* and *Mnium hornum* become locally dominant.

The position in B is much the same except that the field layer is still less well represented both in species and individuals. Typical C (beechwoods) is a single layered community, only locally does *Oxalis* form a continuous carpet and again on wind-swept margins bryophytes (*Dicranum scoparium*, *Eurhynchium myosuroides*, *Mnium hornum*) form a continuous ground stratum.

(4) *Height growth and density of beech in the beechwoods and the relative vigour of some other species.*

The beeches of A_0 are magnificent trees, 107 ft. high, with the clean whitish grey bark associated with vigorous growth. In A the range of height is from approximately 70 to 90 ft. with an average of 82 ft. For the most part the stems are well grown and of good form. In B the average height is 70 ft., while in C the growth is poor (60 ft.), and the stems are often crooked and dark in colour. Running *pari passu* with decreasing vigour there is an increase in the hardness of the bark, and while rough, shallow fissured bark is not confined to B and C it is commoner here than elsewhere.

The number of stems per 10,000 sq. ft. shows an increase from A_0 to C (20, 40, 52, 93) and a similar gradation in the number of dominants (15, 24, 33, 43) with a corresponding decrease in the girth at breast height of dominant beeches 64½, 43½, 37½, 29½ in.

The oak (*Quercus robur*) accompanying the beech has a height approximately the same as the beech, but in C the crowns of some oaks project above the general level of the beech crowns and on the whole show slightly better growth, straighter stems and thicker trunks. Ash in A_0 and A attains the full height of the canopy and grows very well: as also does sycamore in sere A. Comparative measurements are lacking for other woody plants, but *Corylus*, *Sambucus* and *Euonymus* show exceptional height growth in A_0.

The height and density of *Rubus* vary according to the shade and the sere, but in the beechwoods of A, *Rubus* is more vigorous with an average height from 18 to 24 in.; in B from 15 to 18 in.

(5) *The succession.*

The existing data are too meagre to justify final conclusions respecting the scrub, but *Prunus spinosa* and *Crataegus monogyna* form scrub in A_0 and A and juniper locally in C (and B?). Although birch (*Betula alba*, *B. pubescens* and hybrids) is present in all the seres, the absence of a definite birchwood in the early stages of the succession is noteworthy although on Ivinghoe Common open birchwood follows *Calluna*. Similarly in the communities examined hornbeam plays no part in the succession. The stage normally following scrub is ash-oakwood in A_0 and A and oakwood in B and C, the ash playing a more important part in A_0 than in A; but the communities available for study do not decide whether the ash would hold its own with oak and maintain itself co-dominant with the latter in stable woodland. The evidence from A is also negative, but the chances of ash suppression by oak are greater and it is probable that the developing woodland of ash and oak would normally lead to almost pure oakwood. Invasion by beech leads to the beech associes and finally to beechwood in which ash and oak in A_0 and A and oak in B and C remain as constant although infrequent members.

These differences emphasise the conclusion reached respecting the habitats of the four seres. Although the soils are highly acid, there is a steep gradient of fertility demonstrated by the size of plants common to all and by the species distribution determined by the soil within the limits imposed by shade. Yet nitrification is possible in all, although in the gaps of beechwoods belonging to type C it may be temporary only.

DESCRIPTION AND ANALYSIS OF THE VEGETATION ON THE COMMONS AND OF THE FOUR SERES.

The vegetation of the commons.

Fourteen commons have been investigated. Their size varies from a few acres to several hundred, their soils from calcareous (local) to loamy and silty, and their vegetation from calcicolous to markedly "acidic." There is no correlation between area and uniformity of vegetational cover; abrupt changes are met with even on small commons, whilst a uniform vegetation may occupy nearly the whole of large commons.

There are three major facies dominated respectively by grasses and herbs, by bracken and by heather. No separate lists were made for these three and altogether 141 non-woody species and fourteen mosses are recorded. Species with high constancy and/or high average frequency are listed below.

Species, exclusive of woody plants, with constancy 4 and 5 and/or average frequency of 2·1 and over, from fourteen commons.

With constancy 5.

	Average frequency
Pteridium aquilinum	4·6
Agrostis vulgaris	3·9
Holcus lanatus	3·4
Anthoxanthum odoratum	3·1
Holcus mollis	3·0
Potentilla erecta	2·9
Festuca rubra	2·7
Galium saxatile	2·6
Hypocharis radicata	2·3
Trifolium repens	2·3
Plantago lanceolata	2·2
Achillea millefolium	2·1
Lotus uliginosus	2·1
Cirsium palustre	2·0
Dactylis glomerata	2·0
Hieracium pilosella	2·0
Lotus corniculatus	2·0
Potentilla sterilis	2·0
Rumex acetosa	2·0
Stellaria graminea	2·0
Ranunculus repens	1·9
Sieglingia decumbens	1·9
Arrhenatherum elatius	1·8

With constancy 4.

	Average frequency
Cynosurus cristatus	2·4
Epilobium angustifolium	2·4
Digitalis purpurea	2·2
Luzula erecta	2·1
Poa trivialis	2·1
Campanula rotundifolia	2·0
Hypericum pulchrum	2·0
Prunella vulgaris	2·0
Veronica chamaedrys	2·0
Galium verum	1·9
Poa pratensis	1·9
Rumex acetosella	1·9
Veronica officinalis	1·9
Viola canina	1·9
Cirsium arvense	1·7
Deschampsia caespitosa	1·7
Cerastium vulgatum	1·6
Senecio jacobaea	1·6
Polytrichum formosum	2·3
Hylocomium squarrosum	2·0

With low constancy in brackets and high local frequency.

Calluna vulgaris (3)	2·9
Agrostis canina (2)	2·6
Deschampsia flexuosa (1)	2·5
Hypnum schreberi (2)	3·1
Thuidium tamariscinum (1)	3·0
Mnium hornum (2)	2·6
Hypnum cupressiforme (2)	2·5
Polytrichum juniperinum (2)	2·5

The grassland facies.

The part of the commons which seems to have at least a relative permanence is the grazed pasture which consists essentially of a closed mat of perennial grasses and herbs with few mosses. The bulk of the species occur here: the chief constituents are *Agrostis vulgaris*, *Anthoxanthum odoratum*, *Cynosurus cristatus*, *Festuca rubra*, *Galium saxatile*, *G. verum* (occasional or locally frequent), *Holcus lanatus*, *H. mollis*, *Potentilla erecta*, *Trifolium repens*; but there are many species of low average frequency which collectively contribute appreciably to the richness of certain of the pastures. The general appearance is "dry" and "acidic," but the presence of more exacting species like *Achillea millefolium*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Lolium perenne* (constancy 3, average frequency 2·0), *Poa pratensis* and *Trisetum flavescens* (3 and 1·4) puts the level of fertility much higher than that of typical heath. On the other hand there is no close kinship to chalk grassland, although locally on chalk outcrops, but contributing little to the pasture as a whole, are to be found *Agrimonia eupatoria*, *Brachypodium silvaticum*, *Briza media*, *Bryonia dioica*, *Cirsium acaule*, *Helianthemum chamaecistus*, *Koeleria gracilis*, *Linum catharticum*, *Poterium sanguisorba* and *Tamus communis*. Again quite locally on damper soil there occur *Alopecurus geniculatus*, *Juncus effusus* and *J. conglomeratus*.

Differences on a larger scale and occasionally relating to nearly whole commons correspond with differences in soil type. For example, the floristically poor Naphill Common is the only one to show *Genista anglica* and *Deschampsia flexuosa*, which is occasional to locally abundant, and here too *Festuca ovina* is more frequent than on any of the six commons from which it is recorded. Again *Sieglingia decumbens* has the higher frequency from the poorer commons of Naphill, Berkhamstead and Coombe Hill. On the other hand the more exacting species are more conspicuous on the more fertile Great and Little Hampden Commons. The only mosses with high constancy (4) are *Hylocomium squarrosum* and *Polytrichum formosum*, and all are local.

The bracken facies.

Bracken is the most abundant single species. It covers nearly the whole of Berkhamstead Common, large parts of most commons, and is absent only from Balham's Common, the whole of which is pastured; only on parts of Naphill does the soil appear to be marginal for *Pteridium*. The bracken varies much in vigour, density and associated species, and all three are probably affected locally by burning and cutting of the bracken. Near its existence limit on Naphill the bracken is isolated, 12–18 in. high growing among dominant *Calluna* which is only 3–4 in. high. On Berkhamstead Common, where large areas have been burned over, the open bracken is about 24 in. high and is accompanied by a poor flora but rich in individuals of *Agrostis canina*, *A. vulgaris*, *Potentilla erecta* and *Sieglingia decumbens*. Below the 4 ft. bracken on

Ibstone Common low-growing *Rubus fruticosus* is frequent, and even under the 6 ft. bracken on Great Hampden Common are to be found *Galium saxatile*, *Lonicera periclymenum* and small *Rubus*. Elsewhere *Holcus mollis* and *Scilla non-scripta* have been recorded. Uncut and unburned bracken varies from 12 to 72 in. in height; this indicates a wide range of soil conditions.

The Calluna *facies.*

Similar and corresponding differences are found in the vigour of *Calluna*, which is short where bracken is short and tall (18 in. with a maximum of 36 in.) where bracken is 66 in. high. *Calluna*, however, is not so widespread; it is found on six commons only and occupies smaller areas. Its chief companion is *Hypnum schreberi*, but the nitratophilous *Epilobium angustifolium* and *Rubus idaeus* have been noted growing mixed with vigorous *Calluna*. The absence of *Erica cinerea*, *E. tetralix* and *Vaccinium myrtillus* is noteworthy.

The present limits of the three facies are partly determined by biotic factors (cutting and burning of bracken, burning and grazing of heather and grazing of the pasture by cattle, horses, sheep and rabbits). We may suppose that at one time these grass heaths were more intensively utilised for pasturage by the commoners than now and that invasion by bracken and heather was kept in check. With the change in economic conditions and the lack of necessity to maintain the commons as pastures, invading bracken and heather made headway, both supplanting the pasture, and bracken suppressing the heather at least on the better soils. But direct and indirect human interference checks the natural process and alters the constitution of the separate communities and the vigour of the dominants.

While due allowance must be made for modifications induced by the biotic factor, it is also clear from the behaviour of intact bracken and heather and the different complexes of grasses and herbs forming the pasture that the various facies are not uniform among themselves but reflect considerable soil differences. To assign each community to its respective sere on the available soil and vegetational data is premature, but as an aid to their discrimination the accompanying tabulated summary is offered as a somewhat arbitrary guide.

Grassland	Sere A Richer in the more exacting species	Sere B Intermediate	Sere C Richer in "heathy" grasses and herbs
Average height of *Calluna*	18 in.	10–12 in.	6 in.
Average height of *Pteridium*	6 ft.	4 ft.	1–2 ft.

Woody vegetation.

The woody species are considered in two groups, (1) shrubs, representing a potential scrub and (2) tree invaders.

(1) *Shrubs.* The potential scrub is characterised by its comparative floristic poverty. Only twenty-six species occur as against forty-eight for the escarpment, and most of these have low frequency and constancy values: only ten

have high values. With constancy 5 and the average frequency given in brackets there are *Ulex europaeus* (3·0), *Crataegus monogyna* (2·5), *Rubus fruticosus* (2·5), *Lonicera periclymenum* (2·3), *Rosa canina* (1·9), and *R. arvensis* (1·7); with constancy 4, *Prunus spinosa* (2·5), *Sambucus nigra* (2·1), *Solanum dulcamara* (1·7), and *Corylus avellana* (1·6). *Ulex* with a frequency never less than occasional is often locally abundant to locally dominant and may cover considerable areas. Its former use as fodder for cattle is no doubt responsible for its present status which is largely maintained by human interference with the natural vegetation. These gorse communities are often burned, and the state of the succeeding vegetation will vary according to the date of the last burning, the invading species and other factors. *Holcus lanatus* is often locally dominant here. *Crataegus* and *Prunus spinosa* occur scattered or forming dense thickets of small extent, but one gets the impression that apart from the check to establishment by grazing, free colonisation is inhibited in some way: certainly there is not the same free invasion that occurs on the South Downs plateau when grazing pressure is lifted. On the Chiltern plateau the freest colonisation is found on derelict, moderately grazed pasture. The high local frequency of *Rubus* is associated with overhead canopy, either of trees or bracken, there being no evidence of its power to assume or maintain dominance in the open, where the bramble is represented by occasional individuals or clumps.

Soil differences are again obvious in the local or rare occurrence on the more fertile soils of *Acer campestre, Cornus sanguinea, Rhamnus catharticus* and *Viburnum lantana.* Juniper (the upright or spreading but not the procumbent form) is confined to Naphill Common and Coombe Hill, *Sarothamnus scoparius* is rare and *Sambucus nigra* is found near rabbit burrows and on the better soils. *Sarothamnus, Crataegus oxyacantha, Prunus domestica, Rosa tomentosa, Salix cinerea* and *S. aurita* are not recorded from the escarpment.

(2) *Tree invaders.* Over most of the commons adult trees—oak, ash, beech, elm—are found isolated and in groups. The isolated trees have a pioneer form and may be spontaneous or planted, but the groups of beech and elm appear to be planted. The fact that most of the adult trees remain isolated shows that conditions for regeneration have been and are now unfavourable. Only on Naphill Common has there been a general colonisation by beech and oak from parent trees of pioneer form now included in the young wood.

Quercus robur (constancy 5) is easily the most successful tree invader: it is present on all the commons with a frequency varying from occasional to locally dominant. Ash (constancy 5) and beech (4) come a poor second in number of individuals, although a similar variation in frequency is met with: the restriction of both to the boundaries of some commons bears witness to the difficulties experienced in colonisation. The naturalised alien *Acer pseudoplatanus* (3) is not so widespread but is locally successful. The scarcity or local abundance only of some native trees is a surprising feature of the Chiltern plateau:

Betula spp. are on the whole rare or occasional, but *Betula alba* is locally dominant on Ivinghoe Common; *Carpinus betulus* has also a low frequency and is found on six commons only, on three of which it is marginal: *Ilex aquifolium* is more widespread but with a low frequency; *Populus tremula* is found on two only and is locally dominant on one; *Prunus avium*, with constancy 3, is locally dominant in one small patch but usually occasional. *Sorbus aria*, *S. aucuparia* and *Taxus baccata* all have low constancy and frequency values. Planted trees like *Aesculus hippocastanum*, *Larix decidua*, *Pinus silvestris* and *Picea abies* are rare.

The relative importance of the chief trees in the succession on the plateau is partly elucidated by a study of the relation of these trees to the three facies of the open common and to scrub.

The relation of trees to grassland.

The establishment of trees in pasture meets with difficulties, among which grazing would appear to be only one. No seedlings of beech, hornbeam, ash or birch have been seen; oak seedlings on the other hand are occasional, and successful establishment occurs in societies of *Holcus mollis*. Seedlings of oak and beech produce relatively long tap roots; ash, hornbeam and birch have much weaker tap roots, and it is suggested that the closed mat of pasture may prevent the seedlings getting a firm hold of the soil before the onset of spring droughts. Certainly inside the developing woodland, rooted in beech humus or in mineral soil, ash seedlings, as well as seedlings of hawthorn and holly, are abundant. It may be further suggested that spring frosts will differentiate against the beech seedling, leaving the oak as the first successful invader.

The relation of woody plants to the Calluna *facies.*

Oak, beech, birch, aspen, pine, hawthorn, blackthorn and elder are found invading the *Calluna* facies. Of these oak is the most frequent and the only tree found in the short *Calluna* on Naphill Common, whilst birch successfully invades and suppresses the heather on Ivinghoe Common.

The relation of woody plants to the Pteridium *facies.*

The practice of cutting or burning bracken discriminates in favour of the bracken and against woody plants. Intact bracken checks ecesis of woody plants in at least two ways, by the shade it casts and by the mass of tangled fronds which every year weigh down weak young plants. The shade cast depends on the density of the bracken and in open bracken birch can establish itself, although the phenomenon is local. The second factor operates against ash. No beech or hornbeam was observed established in bracken: as in the pasture and in heather, oak is the most successful and practically the only invader of bracken, even when this is at least 3 ft. 6 in. high. Young oaks form a peripheral curtain, skirting pioneer beech where the density and vigour of the bracken are reduced. The same relation is observed between young birch and oak pioneers in bracken.

Bracken also prevents a general invasion by scrub, and on Coombe Hill the interesting observation was made that no invasion by hawthorn of the locally dominant bracken occurs, whereas hawthorn freely invades adjoining locally dominant bramble.

The relation of trees to scrub.

The practical value of scrub for successful invasion by trees is shown by the fact that at least five out of the six developing woodlands which have become established on these commons have utilised scrub. This is proved by the dead remains of *Crataegus* and *Prunus spinosa* below older trees and the presence of young trees in the zone of scrub fringing the woodland. *Ulex* scrub is not generally invaded by trees: only in one example (sere A) does it appear to have assisted in the formation of woodland, but oak saplings kept nibbled down do occur among mixed pasture and low-growing *Ulex* (2–3 ft.), and on Aldbury Common birch grows successfully in *Ulex* scrub. In this instance it is possible that the birch colonised burnt-over gorse and that birch and gorse grew up side by side.

The developing woodland (seres A_0 and A).

Although scrub is commonly associated with developing woodland, it is not always clear that the initiative lies with scrub. For the difficulties attending the establishment of trees appear to hold for hawthorn as well. In the litter under pioneer beeches of whose conditions of establishment we know nothing, numerous seedlings of hawthorn and holly are found. Most of them die, but the seedlings at the circumference of the shaded area find a light intensity adequate for survival and growth. The fringe of oaks round a pioneer beech and of birch round a pioneer oak, already mentioned, are comparable examples. Once established lateral spread of the hawthorn follows by the creation of conditions marginal to itself similar to those provided by the pioneer beech. Within the scrub thus formed ash comes up freely.

The structure of the developing ash-oakwood on Little Hampden Common is in line with this interpretation, although it does not disprove the possibility of the establishment of the pioneer in scrub. It consists essentially of an old dead pioneer beech (F_1) surrounded by oaks, beeches (F_2 and F_3) and ash, below which is dead scrub. The advancing margin consists of scrub and young ash; in the bracken beyond are scattered sapling oaks. The advance of scrub and of woodland from the edge of the woods adjoining Great Hampden Common may be explained in the same way.

Suitable conditions for germination in the broken cover in the neighbourhood of a pit would appear to explain the origin of the developing woodland on Downley Common. The woodland consists of all forms and ages of oak and beech, but the beech pioneers are older and more numerous. Here, as certainly in the developing woodland near Hill Farm, where the soil has been disturbed, scrub can equally well become established and serve to protect young trees. The example on Naphill Common already mentioned shows that woodland can spread without the aid of scrub.

The absence of a general colonisation of the commons by scrub such as is found on derelict enclosed pasture does not exclude the possibility of scrub playing its normal part in the spread of woodland in the absence or amelioration of those inhibiting factors associated with direct and indirect human interference. But the scarcity and localisation of scrub and of developing woodland emphasise the difficulties experienced in its establishment.

The structure of six out of the eight examples examined which are not too mature to have lived down their early associations is in essence that outlined for the developing woodland on Little Hampden Common, and different from the expectations raised by the fact that oak is the most successful coloniser of the different facies of the commons. It seems likely that the Naphill Wood or parts of it did in fact arise in this way, but the early association with beeches led to the formation of a mixed wood (associes, *vide* p. 477) in parts only of which is oak dominant. The differences may be ultimately due to differences in the soil, acting through the vegetation cover, for the Naphill Wood belongs to seres B and C, while the rest belong to seres A_0 and A; and these are the only examples discussed here.

The barriers to the free spread of scrub result in the telescoping of the communities which normally follow and in the appearance of a compact community in which the transition from pasture to woodland is abrupt, rather than of a diffuse community in which it is gradual. Moreover, the change is almost complete, for few of the normal constituents of the pasture survive under the shade cast by the scrub and the trees, and the plants which appear when the wood opens out are typical woodland species. The more important exceptions are facultative shade species like *Agrostis vulgaris*, *Holcus mollis*, *Pteridium*, and *Rubus fruticosus*. The last is important, for whereas on the open commons it is patchy and brown, under shade it tends to form a continuous layer and is much darker green and more vigorous.

The early history of the developing woodland outlined above explains the spatial distribution of the ash, oak and beech in the younger examples where these three trees, of different age, size and form, are ranged round pioneers of oak and beech. Ash as a pioneer is rare. In the two relatively mature and larger examples, where development has been made possible either by a more rapid development and colonisation of scrub by ash and oak or by a delayed advance of the beech, ash and oak together form the canopy. All three species reproduce themselves, ash most freely, particularly in A_0 where thickets of sapling ashes show a vigorous growth, though retarded in some individuals by the attacks of *Chionaspis salicis* on the stem and of *Prays curtisellus* on the leading buds. Beech is always present but multiplies less freely than either ash or oak. Locally *Acer pseudoplatanus* freely invades the scrub, forming thickets of saplings and well-grown poles, while *Prunus avium* has a high constancy but a low average frequency in A. Altogether there are fourteen phanerophytes in A_0 and thirty-three in A.

Towards the making of a shrub layer in the maturer examples *Crataegus* and *Prunus spinosa*, locally abundant or locally dominant at the margins, contribute little or nothing. *Corylus*, with constancy 5 in A, is never more than occasional, although sometimes locally frequent in A_0; *Sambucus*, frequent to locally dominant in exploited woodland of A_0, is occasional and has the highest constancy value in A; *Cornus* and *Ligustrum*, both with low constancy and frequency values, are found only in A, while *Euonymus* (o.) is confined to A_0. These together with *Acer campestre, Rosa arvensis, Salix caprea* and *Viburnum opulus*, which have low frequencies only, fail to form anything like a continuous shrub layer. In a lower layer *Lonicera* (constancy 5, average frequency 2·8) and *Rubus* (5, 3·3) in A are much more successful, whilst in A_0 their distribution is much less general, although *Rubus* may be locally abundant. In A_0 some of the shrubs show remarkable growth; *Crataegus* in partial shade attains 40 ft., *Prunus spinosa* 23 ft., while *Corylus, Euonymus* and *Sambucus* reach 20, 12 and 15 ft. respectively.

Between these communities, so few in number, so varied in degree of development, where migrations are incomplete, where shade varies so much from place to place, where no stable condition in the field layers has been attained, and where no critical examination of the variations has been made, detailed comparison of the field layers is out of the question. In particular no deductions can be made from the absence of species.

The flora of the field layer is mixed; exacting species (*Asperula odorata, Circaea lutetiana, Mercurialis perennis, Nepeta glechoma, Sanicula europaea, Catharinea undulata, Mnium undulatum*) predominate; tolerant species (*Deschampsia caespitosa, Oxalis acetosella, Pteridium aquilinum, Eurhynchium praelongum*) strong in individuals, form a small proportion of the total number of species, while acidiphilous species, *Conopodium denudatum, Stellaria uliginosa* (A_0), *Galium saxatile, Potentilla sterilis, Holcus mollis, Scilla non-scripta, Dicranella heteromalla* (A_0, A), *Anthoxanthum odoratum, Digitalis purpurea, Potentilla erecta* (A) are present in one or other or both seres. But *Calluna vulgaris, Deschampsia flexuosa, Hypnum schreberi* and *Leucobryum glaucum* are absent. The floristic composition of the vegetation as a whole indicates a fertile soil.

The species with higher frequency values (more than occasional), listed and arranged in life-form classes on p. 471, emphasise these features, and among acidiphilous species only *Holcus mollis* and *Scilla* attain the higher values of constancy or average frequency. In distinguishing the seres the higher frequency of *Mercurialis* and of *Scilla* in A_0 has real significance; in A_0 mercury

Species with high constancy and/or high frequency in the developing woodland of seres A_0 and A.

		A_0 2	A 6 for woody plants and 4 for herbs, etc.	
Life form	Number of examples	Frequency	Constancy	Frequency
P.	Fraxinus excelsior	f.-l.d.	5	o.-d.
P.	Quercus robur	f.-a.	5	f.-a.
P.	Fagus silvatica	o.-l.a.	5	r.-l.d.
P.	Acer pseudoplatanus	o.-l.d.	4	o.-l.a.
P.	Prunus avium	—	5	o.
P.	Ilex aquifolium	—	4	o.
P.	Sambucus nigra	f.-l.d.	5	o.
P.	Crataegus monogyna	r.-l.a.	5	o.-f.-l.d.
P.	Prunus spinosa	o.-l.a.	5	o.-l.a.
P.	Corylus avellana	o.-l.f.	5	o.-l.f.
P.	Rosa arvensis	r.	4	o.
P.	Lonicera periclymenum	o.-l.f.	5	f.
P.	Hedera helix	—	3	o.-l.a.
Ch.	Lamium galeobdolon	o.-f.-l.a.	2	l.d.
Ch.	Nepeta glechoma	f.-a.-l.d.	5	o.-f.
Ch.	Veronica chamaedrys	o.	4	o.-l.f.
Ch.	V. montana	o.	2	f.
H.r.	Dryopteris filix-mas	o.-l.f.	3	o.-f.
H.r.	Fragaria vesca	o.-f.	4	o.-l.f.
H.r.	Oxalis acetosella	f.-l.a.	5	r.-l.d.
H.r.	Sanicula europaea	l.	4	r.-l.d.
H.r.	Viola silvatica	o.	5	r.-f.
H.s.	Ajuga reptans	o.	4	o.-f.-l.a.
H.s. (G.r.)	Epilobium angustifolium	l.f.	3	o.-l.a.
H.s.	Geum urbanum	o.-f.	4	l.-f.
H.s.	Mercurialis perennis	f.-l.d.	2	o.-l.f.
H.s.	Digitalis purpurea	—	4	o.
H.s.	Ranunculus repens	l.	4	o.-l.
H.s.	Rubus fruticosus	o.-l.a.	5	o.-f.-l.d.
H.s.	R. idaeus	o.	2	o.-f.
H.s.	Urtica dioica	o.-l.a.	3	l.f.
H.c.	Brachypodium silvaticum	o.	4	l.
H.c.	Deschampsia caespitosa	o.-l.d.	4	o.-l.a.
H.c.	Festuca gigantea	r.	4	o.-l.
H.c.	Holcus lanatus	o.	4	o.
H.c.	Juncus communis	l.a.	—	—
H.c.	Poa trivialis	o.-f.	4	o.-l.
G.r.	Asperula odorata	o.l.	4	f.-a.-l.d.
G.r.	Circaea lutetiana	o.-l.f.	4	o.-f.-a.
G.r.	Holcus mollis	o.l.	4	o.-l.f.
G.r.	Pteridium aquilinum	o.-f.-l.d.	5	o.-f.-l.d.
G.b.	Scilla non-scripta	f.-l.a.	5	o.-l.f.
T.	Arenaria trinervia	o.-l.f.	4	o.
T.	Geranium robertianum	—	4	o.-l.f.
	Brachythecium rutabulum	o.-f.	2	o.
	Catharinea undulata	f.-l.d.	4	o.-l.a.
	Dicranella heteromalla	o.-f.	4	r.-l.d.
	Eurhynchium piliferum	l.f.	2	f.
	E. praelongum	f.	4	f.-a.
	E. striatum	o.-f.	3	o.-f.
	Mnium hornum	o.-f.	5	o.-f.
	M. undulatum	f.	4	o.-f.
	Polytrichum formosum	—	4	l.f.
	Thuidium tamariscinum	o.-l.f.	4	f.

up to 20 in. is frequent to locally dominant; in A it is of smaller growth, and occasional to locally frequent in one example only. *Scilla* on the other hand is frequent to locally abundant in one example of A_0, but is found in all four examples of A, though with a frequency never more than occasional to locally frequent.

Since no intensive examination has been made of the developing field layer either in its immature or in its mature state no conclusions can be drawn about the representation of the different life-form subclasses and their relationships during development in the contrasted seres. But the spectra of all species of the developing woodland of the two seres demonstrate the predominance of scapose hemicryptophytes in A_0 and the approach of caespitose hemicryptophytes to equality with them in A.

Biological spectra of all species in the developing woodland of seres A_0 and A, calculated with and without phanerophytes.

Sere	P.	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	T.	Total
(*a*) Including phanerophytes.									
A_0	23 (15)	11 (7)	14 (9)	21·5 (14)	14 (9)	7·5 (5)	3 (2)	6 (4)	100 (65)
A	30·5 (33)	8·5 (9)	8·5 (9)	19·5 (21)	17 (18)	9·5 (10)	3 (3)	3·5 (4)	100 (107)
(*b*) Without phanerophytes.									
A_0	—	14	18	28	18	10	4	8	100
A	—	12	12	28·5	24·5	13·5	4	5·5	100

The chamaephytes are all herbaceous evergreens. The high frequency of *Nepeta glechoma* and perhaps of *Lamium galeobdolon* are indicators of youth, as is also the numerical strength both in species and in individuals of the rosette hemicryptophytes, which, unless tall (like *Dryopteris*) or seasonally complementary with the tall hemicryptophytes and rhizome geophytes with leafy stems, would certainly be excluded by these taller growing plants did they cover a wider area. Most of them have a low frequency or a high local frequency only, but *Mercurialis*, *Geum* and *Pteridium* in A_0, and *Ajuga*, *Rubus* spp., *Pteridium*, *Asperula* and *Circaea* in A, have higher values. Similarly none of the grasses has a really high frequency.

On the whole the spectra and the whole set of species of the field layer indicate the potentialities of the habitats and communities in a state of development, apparently leading to woodland in which a field layer of tall forms would be conspicuous.

The oakwoods (A_0, A, B).

The developments forecast for the subsidiary vegetation of the developing woodland do not materialise in full in the oakwoods examined, for the bulk of these appear to be planted and not yet to have attained maturity. Their uniform height, purity of tree layer with occasional exotic conifers, replacement of *Quercus robur* by *Q. sessiliflora* in one example and partial replacement by *Quercus cerris* in another, all indicate the hand of man. By itself oak planting on land formerly occupied by developing woodland or by oakwood, while determining the composition of the tree layer, would not appreciably influence the eventual constitution of the ground vegetation, but there is no clear evidence that this happened. Planting on abandoned agricultural land whose soil properties are considerably altered as the result of cultivation may have taken place; in fact in one wood the ground is plainly ridged. In short, these oakwoods cannot be regarded as the lineal descendants of the developing woodlands. Probably they never are, and while they may be taken as representing the next stages in the general succession, their identity with the corresponding stage which would develop naturally cannot be taken for granted.

The scarcity of oakwood is remarkable, all the more so because oak is a constant constituent of the beechwoods and, as we have seen, is the most successful coloniser of the commons. Two oakwoods in A_0, six in A and seven in B have been examined. They possess neither the floristic richness nor the structural complexity of the Damp Oakwood nor the severe simplicity of the Dry Oakwood. They form a series running alongside but not merging with them. *Quercus robur* is dominant; *Q. sessiliflora* accompanies it as an occasional constituent in woods of both the A and the B seres, replacing it in one B wood. Estimates of their height have little value because the trees in different woods are of different ages and no stem analyses have been made; but in A_0 magnificent oaks, 80 ft. high, have a girth at breast height of 8 ft. 1½ in. In A and B their height varies from 65 to over 80 ft., figures that are not to be taken as maxima. Ash is a normal constituent of A_0 and A woods, frequent in A_0, occasional in A and exceptional in B. In A_0 its growth is excellent, relatively young trees attaining 77 ft., while the bark is still relatively thin and green, just showing the beginnings of fissuring. It is exceedingly doubtful if the natural wood of A_0 and A is pure oak: a higher percentage of ash would be expected both from its high frequency in the developing woodlands and its vigour and free regeneration in the oakwoods. Its scarcity is further evidence of planting. *Acer pseudoplatanus* is abundant here and there in all three seres, in A_0 forming locally a subcanopy to oak and in vigour running parallel with ash and oak. *Prunus avium* is rare to occasional in all, while *Carpinus betulus* is recorded from three examples only (A and B), in two of which it is marginal, in the third occasional. Beech is found in all, both in canopy and as saplings contributing to the scanty shrub layer.

The failure to form a shrub layer, noted for the developing wood, is again evident in the oakwood. Even in A_0, where something of the kind might be expected, the layer is floristically poor and is represented by occasional to frequent *Corylus*, frequent to abundant *Sambucus*, individuals reaching 20 ft., and *Ribes rubrum*, locally abundant in one wood. *Euonymus* (r.) and *Rosa tomentosa* (o.) are confined to A_0. In A there are more species: significant types are *Corylus* (constancy 5, average frequency 2·5), *Crataegus* (5, 2·1), *Viburnum opulus* (5, 2·0), *Ilex* (4, 1·8), *Rosa arvensis* (4, 1·8), *Hedera* (3, 2·2), *Ligustrum* (1, 3·0), while with low values and confined to A are *Cornus*, *Solanum* and

Tamus. This generalisation about the shrub layer breaks down in two woods; in the wood on ridged soil where *Castanea*, *Corylus* and *Fagus* form an open shrub layer with *Corylus* locally abundant, and in part of another with affinities to A_0 where *Corylus* is locally dominant. Planting has probably taken place in both. In typical B there is no proper shrub layer, which is only represented by *Corylus*, *Crataegus* and *Ilex*, each with a high constancy but low frequency.

The place of the shrub layer is taken by *Lonicera* and *Rubus*, both of which are well represented in A_0, A and B. *Lonicera*, with an average frequency of 2·8 and 2·9 and the highest constancy value in A and B, is, however, more consistently abundant in these two types than in A_0, where it is more patchy, though occasionally locally abundant. The same is true for *Rubus*, which fails to form a continuous layer in A_0, but with constancy 5 has average frequencies of 4·2 and 4·8 in A and B respectively.

The *Rubus* layer by its formation of an evergreen canopy must influence the number of species and individuals in the field layer and prevent the continuity and the competition for place between species of different life forms that one normally expects in oakwood. In point of fact the number of species differs little from that in the corresponding developing woodlands. In A_0 there are 57 herbs and 12 bryophytes, in A 75 and 24 and in B 45 and 17. As there are only two examples of A_0 fair comparison can be made between A and B only. But again we note the prevalence in A_0 and A, of exacting herbs, occasionally present but quite local or rare in B, the occurrence, often with quite high values, of tolerant species such as *Deschampsia caespitosa*, *Oxalis*, *Pteridium*, in all three, and the presence of acidiphilous species in any one, two or in all three. Of these may be mentioned *Conopodium* (A_0, B), *Potentilla erecta*, *Galium saxatile*, *Carex pilulifera*, *Blechnum*, *Anthoxanthum* (A, B), *Hypericum pulchrum*, *Stachys betonica*, *Deschampsia flexuosa*, *Calluna* (B), and *Potentilla sterilis*, *Holcus mollis*, *Digitalis purpurea* in all three. Among those exclusive to any one sere are *Cardamine flexuosa*, *Heracleum sphondylium*, *Paris quadrifolia*, *Filipendula ulmaria* (A_0), *Anemone*, *Arum*, *Listera ovata*, *Melica uniflora*, *Polygonatum multiflorum*, *Stachys silvatica* (A) and *Deschampsia flexuosa*, *Calluna*, *Stachys betonica*, *Hypericum pulchrum* (B).

The influence of *Rubus* on the field layer will be more fully described for the beechwoods; meanwhile it is of some significance to note the effect of the canopy of trees and shrubs on *Rubus* and *Scilla* respectively. Under a canopy of oak and continuous *Corylus*, *Scilla* only is found; under oak and more open *Corylus*, *Scilla* is accompanied by small scattered *Rubus*.

The data (Table II) give the distribution of the life forms of species confined to one sere, to any two, and present in all three. They show the large contribution made to the vegetation of B by species common to all three types of oakwood. The life forms represented give a strong bias to the spectra of the different seres, the greater where the total number of species is small, as in B, and the less where large as in A. The data bring out the closer relationship between A_0 and A than between A_0 and B, and the emphasis on different life forms when A_0 and A (scapose hemicryptophytes) and A and B (caespitose hemicryptophytes) are compared. Also the actual species of scapose hemicryptophytes exclusive to A_0, A and B are of course different.

Table II.

Distribution of life forms of species exclusive to any one sere or any combination of seres in the oakwoods of A_0, A and B.

	P.	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	T.	Total
A_0, A, B	13	3	5	7	6	5	1	0	40
A_0, A	4	3	5	6	4	0	0	3	25
A, B	5	4	1	1	4	1	0	1	17
A_0, B	0	0	0	0	0	1	1	0	2
A_0	3	0	1	5	0	1	0	1	11
A	7	0	0	4	3	5	2	2	23
B	1	2	0	2	0	0	0	1	6

Biological spectra of all species of the oakwoods of seres A_0, A and B.

	P.	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	T.	Total
				(1) Including phanerophytes.					
A_0	25·5 (20)	8 (6)	14 (11)	23 (18)	13 (10)	9 (7)	2·5 (2)	5 (4)	100 (78)
A	27·5 (29)	9·5 (10)	10·5 (11)	17 (18)	16 (17)	10·5 (11)	3 (3)	6 (6)	100 (105)
B	29 (19)	14 (9)	9 (6)	15·5 (10)	15·5 (10)	11 (7)	3 (2)	3 (2)	100 (65)
				(2) Without phanerophytes.					
A_0	—	10·5	19	31	17	12	3·5	7	100
A	—	13	14·5	23·5	22·5	14·5	4	8	100
B	—	19·5	13	21·5	21·5	15·5	4·5	4·5	100

The spectra of the three types show the general features characteristic of the seres as a whole, except that in B the scapose and caespitose hemicryptophytes are equal in number, a departure which is in some measure accounted for by the bias already noted. This bias loses some of its significance when it is realised that each of the three scapose hemicryptophytes, ***Mercurialis***, ***Rubus idaeus*** and *Scrophularia nodosa*, common to A_0, A and B, occurs in one example only of the B oakwoods and there it is local.

The significant species are few in number (see list of species, p. 476). The herbaceous chamaephytes *Lamium galeobdolon* and *Nepeta glechoma* are confined to A_0 and A, with a high frequency in both. The rosette and scapose hemicryptophytes, except the tolerant *Oxalis* and *Rubus fruticosus*, with significant values in all three oakwoods, are similarly restricted; and on the whole the scapose hemicryptophytes, in particular *Mercurialis*, have higher frequencies in A_0 than in A. Among the caespitose hemicryptophytes there is a clearer separation, with *Agrostis vulgaris* and *Anthoxanthum* significant only in B, the rest in A_0 or A or both. The rhizomatous grass *Holcus mollis* is significant in A and B, while the rhizome geophytes with leafy stems are confined to A_0 and A, *Circaea* having a much higher frequency in A_0 than in A.

The bulbous geophyte *Scilla* is a conspicuous feature in woods of A_0 and A and is local only in B.

Species significant in the oakwoods of seres A_0, A and B.

Sere in which each species is significant	Life form	Number of examples ...	A_0 2	A 6		B 7	
			Frequency	Constancy	Frequency	Constancy	Frequency
		Species significant in all three seres.					
A_0, A, B	P.	Quercus robur	f.-d.	5	4·8	5	4·4
A_0, A, B	P.	Acer pseudoplatanus	o.-l.d.	2	2·3	3	2·3
A_0, A, B	P.	Corylus avellana	o.-f.	5	2·5	4	2·0
A_0, A, B	P.	Lonicera periclymenum	o.-f.-l.a.	5	2·8	5	2·9
A_0, A, B	H.r.	Oxalis acetosella	o.-f.-l.d.	5	2·6	5	2·0
A_0, A, B	H.s.	Rubus fruticosus	o.-f.-l.d.	5	4·2	5	4·8
A_0, A, B	G.r.	Pteridium aquilinum	f.-l.d.	5	2·8	5	3·0
		Dicranella heteromalla	o.-l.a.	4	1·8	4	2·0
		Eurhynchium praelongum	f.-l.a.	5	2·5	3	3·0
		Species significant in one or two seres.					
A_0	P.	Ribes rubrum	o.-l.a.	2	1·0	—	—
A_0	P.	Sambucus nigra	o.-f.	3	2·0	1	2·0
A_0, A	P.	Fraxinus excelsior	f.	5	2·1	3	1·5
A	P.	Ligustrum vulgare	—	1	3·0	—	—
A	P.	Viburnum opulus	o.	5	2·0	—	—
A	P.	Rosa arvensis	r.	4	1·8	3	2·0
A, B	P.	Fagus silvatica	o.	5	2·3	5	2·3
A, B	P.	Crataegus monogyna	r.	5	2·1	4	2·0
A, B	P.	Ilex aquifolium	r.-o.	4	1·8	5	1·8
A, B	P.	Hedera helix	o.	3	2·2	3	2·5
B	P.	Quercus sessiliflora	—	1	2·0	2	3·5
B	P.	Q. robur × sessiliflora	—	2	2·0	3	2·2
A_0, A	Ch.	Lamium galeobdolon	o.-f.-l.a.	5	2·7	—	—
A_0, A	Ch.	Nepeta glechoma	o.-f.-l.a.	4	2·5	—	—
A_0, A	H.r.	Sanicula europaea	o.-f.	4	2·4	—	—
A_0, A	H.r.	Viola silvatica	o.-f.	5	1·9	3	2·0
A	H.r.	Dryopteris filix-mas	o.-l.f.	4	2·0	—	—
A_0	H.s. (G.r.)	Epilobium angustifolium	o.-l.a.	1	2·0	—	—
A_0	H.s.	Geum urbanum	o.-f.	2	2·0	—	—
A_0	H.s.	Urtica dioica	o.-l.f.-l.a.	1	2·0	—	—
A_0, A	H.s.	Ajuga reptans	o.-f.	4	1·8	—	—
A_0, A	H.s.	Mercurialis perennis	f.-l.d.	3	2·2	1	3·0 l.
A	H.s.	Rubus idaeus	o.	2	2·3	1	1·0 l.
A_0, A	H.c.	Juncus communis	o.-f.	1	2·5 l.	—	—
A_0, A	H.c.	Deschampsia caespitosa	o.-f.-l.d.	4	2·0	3	2·0
A	H.c.	Carex silvatica	o.	5	1·8	1	2·0
A	H.c.	Luzula pilosa	r.-l.	4	2·0	1	2·0
B	H.c.	Agrostis vulgaris	—	2	2·0	5	1·7
B	H.c.	Anthoxanthum odoratum	—	1	2·0	1	2·5
A_0, A	G.r.	Circaea lutetiana	f.	5	1·9	—	—
A_0, A	G.r.	Asperula odorata	o.-f.	3	2·5	1	1·0 l.
A, B	G.r.	Holcus mollis	o.-l.f.	5	2·2	5	2·6
A_0, A	G.b.	Scilla non-scripta	o.-f.-l.d.	4	3·3	1	2·0 l.
A	—	Catharinea undulata	o.-l.f.	4	2·0	2	2·0
A	—	Eurhynchium striatum	o.	3	2·2	2	2·0
A	—	Fissidens taxifolius	o.	2	2·3	2	2·0
A	—	Mnium hornum	o.-l.f.	5	2·1	3	2·0
A	—	Thuidium tamariscinum	o.-l.f.	3	2·3	3	2·0

The spectra of significant species, showing approximate numerical equivalence among several life forms are interpreted as indications of immaturity.

	P.	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	Total
A_0	7	2	3	6	2	4	1	25
A	12	2	4	4	4	4	1	31
B	10	0	1	2	2	2	0	17

Among mosses special mention may be made of *Hypnum schreberi*, found only in B oakwoods. Only seven have a high constancy and/or high average frequency: *Dicranella heteromalla* and *Eurhynchium praelongum* are significant in all, while the rest (*Catharinea undulata, Eurhynchium striatum, Fissidens taxifolius, Mnium hornum, Thuidium tamariscinum*) have high values in A.

Reference should be made to a beechwood (High Scrubs) with oak (*Quercus robur, Q. sessiliflora* and hybrids) dominant on the exposed south-west side. Here *Deschampsia flexuosa* is dominant, replaced where the litter lies, as in the Scottish shelterbelt beechwoods (**9**), by *Holcus mollis* and *Oxalis*. The wood has not been examined in detail, but it probably represents an exposed oakwood of sere C.

Coppice is scarce on the plateau as on the escarpment and no attempt has been made to investigate it, but the paucity of species constituting the coppice on the plateau above Kingston is related to the poverty of the shrub layer in the oakwoods and confirms the suggested relationship between them. The standards include oak (d.), ash, birch, beech; the coppice itself is dominated by hazel with oak (f.-l.d.), ash and goat willow being occasional. The spring facies only has been seen: in a newly cut part *Anemone* is frequent to abundant and in the uncut part local, while *Scilla* is locally dominant and *Primula vulgaris* occasional to locally frequent. The coppice is related to sere A and has probably been planted; it is maintained for the rearing of game.

The beech associes (A and B + C).

The examples demonstrating this stage in the succession appear to be natural: some certainly are, others have been modified by human interference in the past, while none is planted. Of the eight examples belonging to A, Hillocks Wood is the largest, while the extensive wood on Naphill Common is mixed B and C.

Hillocks Wood consists of a relatively even-aged mixture of beech and oak, about 112 years old[1]. Many oaks and beeches had double leaders, suggesting coppicing in youth, and owing to the suppression, death and removal of many oaks their number is declining relatively to the beech. Here and there, in and near Hillocks Wood, are patches of oak with moderately large crowns and with an understorey of sapling beech, evenly distributed, even-aged and slowly grown. All these suggest human control: there are no pioneers and it is clear that the even-aged mixture is not a direct unmodified outcome of the invasion of oakwood by beech. Three examples, being parts of East Wood and Penley Hollies, are uneven-aged; oak and beech are irregularly spaced and varied in form, while large stumps of oak and beech are still discernible. In one example, by the felling of the semi-pioneer oaks, the wood is now dominated by beech. These three examples therefore appear to have arisen from the reproduction of pioneer oaks and beeches: there is no evidence that they arose from the invasion of mature oakwood by beech.

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[1] In 1926 a plot of 10,000 sq. ft. had 52 trees in all: 20 dominant beeches, 10 subdominant and 7 suppressed, with 7 dominant and 8 subdominant oaks: while 10 trees each of oak and beech scattered through the wood had average heights of 68 ft. (64–71 ft.) and 72 ft. (66–80 ft.) and average girths of 3 ft. 11¼ in. and 3 ft. 10 in. respectively.

The mixture of pioneer oak and beech is clear enough on Naphill Common. Throughout this large wood, but unevenly distributed, are oak and beech pioneers; many of the latter have been pollarded, measure up to 5 ft. in diameter at the base, and some have rough bark. Some characteristic relationships between oak and beech commonly occur: pioneer beeches (F_1) surrounded by oaks (Q_2) now undergrown by sapling beech (F_3); oak families, with the pioneer oak (Q_1) in the centre, and young beech growing up below; in other places sapling and pole oak and beech grow up side by side and in mixture. In parts adult oak is dominant, in parts beech.

The tree layer consists almost exclusively of oak and beech: in A ash is occasional with a constancy of 3, while saplings are locally frequent; in B + C, ash is local on disturbed soil, where also *Asperula odorata* and *Euphorbia amygdaloides* are found. *Prunus avium* is occasional in both types, with a constancy of 4 in A; while birch is rare and found only in B + C. The hybrid oak is rare in both.

In neither type is a shrub layer present: *Corylus* (constancy 2 and average frequency 2·0), *Crataegus* (4, 2·0), *Ilex* (5, 1·8), *Rosa arvensis* (3, 2·0), *Sambucus* (2, 2·0), *Sorbus aucuparia* (2, 1·0), *Taxus* (2, 1·0), *Viburnum opulus* (3, 1·5) are found in A, all with a low frequency; in B + C the following species occur, *Corylus* (l.), *Crataegus* (o.), *Ilex* (f.-l.a.), *Juniperus* (o.-l.f. in gaps), *Prunus spinosa* (o.), *Pyrus malus* (r.), *Rosa arvensis* (o.), *Salix caprea* (o.), *Sorbus aria* (o.), *Taxus* (o.) and *Ulex* (l.). It is instructive to note that *Ilex*, with abundant seedlings and more seedlings than young plants, is more frequent inside Naphill Wood than on the open common. One *Ilex* reaches a height of 35 ft. Quite rarely dead juniper and blackthorn are found under the canopy, but there is no evidence to show that they have afforded material assistance in the colonisation of oak and beech.

Where there is a double canopy of oak and sapling beech, *Rubus fruticosus*, although numerous, is a small poverty-stricken plant, single stems reaching 15 in. They are ready, however, as has been shown by the recent thinning of Hillocks Wood, to spread and form a continuous layer as soon as the light intensity is adequate. The same is clearly seen in the uneven-aged examples of A; in the young associes where the canopy is dense the ground is devoid of plants except for occasional *Rubus* (6–9 in.) and rare shade *Pteridium*, but in gaps *Rubus* forms dense masses, while in the late associes *Rubus* forms a more continuous layer not confined to gaps. *Lonicera* similarly varies in frequency. In the Naphill associes the frequency and vigour of *Rubus* show a similar response to variation in canopy density; small *Rubus* 4–8 in. high survives under the dense shade of young beech but forms a continuous although open layer about 15 in. high under adult oak, without however showing the dark green and healthy vigour found in the A woods.

What is true for *Rubus* holds in even greater measure for the field layer: under a canopy of trees and *Rubus* few herbs and grasses have a frequency much higher than occasional, except locally. Compared with the oakwoods of A there is a reduction in the number of species from 74 to 63 (vascular plants other than phanerophytes) and from 24 to 18 among bryophytes; in B from 45 and 17 in the oakwoods to 41 and 10 in the associes of B and C. But the numbers and floristic composition of the significant species remain much the same in both A and B (+C) woods respectively.

Exacting species (see list, p. 480) are again in evidence in A and absent or local only in B+C. *Ajuga reptans*, *Angelica silvestris*, *Mercurialis perennis*, *Brachypodium silvaticum*, *Bromus asper*, *Festuca gigantea*, *Lamium galeobdolon*, *Nepeta glechoma*, *Veronica montana*, *Fragaria vesca*, *Primula vulgaris*, *Sanicula europaea*, *Circaea lutetiana*, *Anemone nemorosa*, *Galium aparine*, and *Geranium robertianum* are confined to A, while *Geum urbanum* and *Asperula odorata* are essentially A plants, although both are found, but are local only in B+C. The acidiphilous plants show the same or a similar distribution as in other stages of the corresponding seres: *Melampyrum pratense* and *Pyrola minor* are local only in A, *Anthoxanthum odoratum*, *Calluna vulgaris*, *Deschampsia flexuosa*, *Rumex acetosella* occur in B+C, while *Digitalis purpurea*, *Hypericum pulchrum*, *Potentilla erecta*, *Galium saxatile* and *Holcus mollis* are found in both. The same discrimination is shown among the bryophytes, with *Eurhynchium striatum*, *Fissidens taxifolius* and confined to A, *Hypnum schreberi* to B+C, while *Dicranella heteromalla* is present in both.

The frequency of species of the field layer varies much according to the nature of the canopy, but in most woods it is low and social species like *Holcus mollis* are represented mainly by isolated individuals. The effect of the beech would appear to be first to kill out a number of species by its heavy shade and then, on opening out of the tree canopy, to allow them to come in again, but with a frequency determined by the combined shade of the tree and *Rubus* layers. *Scilla* is an instructive example. In the young associes it is absent from the ground below pioneer beeches but is locally dominant in the intervals between; in the late associes with its continuous *Rubus* layer it is absent. And in fact most of the high average frequency values are due to a high local frequency under pure oak, along wood margins, in paths, and in gaps. Similarly with mosses, for none has a really high frequency except *Polytrichum formosum*, which in Naphill is locally abundant under pure and older beech; in Hillocks Wood its high local frequency is associated with a compact soil and poorer beech growth, and is typical of seres B and C but not of A.

The biological spectra of the beech associes, like the spectrum of the B oakwood, depart from those characteristic of the seres as a whole in that the caespitose hemicryptophytes (16 per cent.) are higher than the scapose

Species significant in the beech associes of seres A and B + C.

Seres in which each species is significant	Life form	Number of examples ...	Sere A 8 Con-stancy	Sere A 8 Average frequency	Sere B + C 1 Frequency range
		Species with significant values in A and B + C.			
A, B + C	P.	Quercus robur	5	4·2	a.-d.
A, B + C	P.	Fagus silvatica	5	4·0	o.-f.-l.d.
A, B + C	P.	Ilex aquifolium	5	1·8	f.
A, B + C	P.	Lonicera periclymenum	5	2·6	f.
A, B + C	H.s.	Rubus fruticosus	5	3·5	f.-a.
A, B + C	G.r.	Holcus mollis	4	2·2	o.-l.a.
A, B + C	G.r.	Pteridium aquilinum	5	2·3	f.-d.
B + C	—	Polytrichum formosum	4	2·1	o.-f.-l.a.
		Species with significant values in A or B + C.			
A	P.	Hedera helix	4	2·2	o.-l.f.
A	P.	Crataegus monogyna	4	2·0	o.
A	P.	Prunus avium	4	2·0	o.
A	Ch.	Lamium galeobdolon	4	2·6	—
A	Ch.	Nepeta glechoma	1	4·0	—
A	H.r.	Dryopteris filix-mas	4	1·8	—
A	H.r.	Oxalis acetosella	5	2·5	o.-l.f.
A	H.s.	Ajuga reptans	4	2·0	—
A	H.s. (G.r.)	Epilobium angustifolium	2	2·3	—
A	H.c.	Deschampsia caespitosa	2	2·3	l.
A	H.c.	Luzula pilosa	5	1·8	o.
A	H.c.	Milium effusum	2	2·3	o.
A, B + C	H.c.	Agrostis vulgaris	4	2·0	o.-f.-l.a.
A	G.r.	Asperula odorata	3	2·3	l.
A	G.r.	Melica uniflora	2	2·2	o.
A	G.b.	Scilla non-scripta	2	2·5	o.
A	T.	Galium aparine	1	3·0	—
A	—	Hypnum cupressiforme	5	2·2	o.
A	—	Catharinea undulata	5	1·9	o.
A	—	Dicranella heteromalla	4	2·3	o.
A	—	Thuidium tamariscinum	4	2·3	l.
A	—	Eurhynchium praelongum	4	2·0	—
A	—	Mnium hornum	4	2·0	o.-l.f.

hemicryptophytes (13 per cent.) in A, and the difference between them in B + C is negligible (10 and 11 per cent.). The significant species are too few to give reliable spectra, hence the spectra given here are based upon all species, omitting those purely local in A and B + C.

Biological spectra of all species, excluding those purely local, in the beech associes of A and B + C.

	P.	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	G.rad.	T.	Total
				(1) Including phanerophytes.						
A	22 (16)	9·5 (7)	11 (8)	14 (10)	21 (15)	11 (8)	3 (2)	1·5 (1)	7 (5)	100 (72)
B + C	36·25 (16)	9 (4)	7 (3)	11·5 (5)	20·5 (9)	9 (4)	4·5 (2)	0	2·25 (1)	100 (44)
				(2) Without phanerophytes.						
A	—	12·5	14	18	27	14	3·5	2	9·0	100
B + C	—	14·5	10·5	18	32	14·5	7·0	0	3·5	100

The differences between the caespitose and scapose hemicryptophytes are now accentuated, a feature abnormal for A but in keeping with the general character of the spectra for B and C. In other respects the spectra are alike but the species are different, the essential distinction lying in the presence of exacting species in A and of markedly acidiphilous species in B + C.

Hillocks Wood was formerly known as "Hillocks Scrubs." With other woods on the Hampden Estate this is said to have grown up from what are locally called "scrubs," enclosed between 1800 and 1840 (information obtained from the working-plan of the Hampden Estate). The name "scrubs" with or without qualification appears in several place-names in the district examined, and it is more than likely that it means exactly what it says. "High Scrubs," repeated twice as the name of existing high forest of oak and beech, has no meaning except in the historical sense, and almost certainly indicates a change from scrub to high forest such as has apparently occurred in Hillocks Wood. Similarly on the South Downs "the Scrubs" is now a high forest of ash and oak which contains within itself evidence of the change. But while the name may have originally been applied to scrub as ecologically understood, it may still without qualification, and without violence to its lay meaning, be applied to coppiced woodland replacing it. Woodland of this kind is found on the plateau above Ellesborough and probably represents an early stage of some of the existing beechwoods or mixed oak and beechwoods. Part of the area is dominated by *Calluna* and *Pteridium*: part consists of coppiced beech, oak (*Quercus robur*), aspen—each locally dominant—hornbeam occasional, and hazel occasional to frequent among the oaks; ash is local. The soil varies somewhat but the shrubs and herbs indicate a wood belonging for the most part to sere A; in particular *Acer campestre, Cornus sanguinea, Sambucus,* and *Solanum*—all occasional only; *Anemone nemorosa* (o.-f.), *Fragaria vesca* (o.), *Geum urbanum* (o.), *Lamium galeobdolon* (o.-l.a.), *Nepeta glechoma* (o.-l.a.), *Scilla* (o.-l.f.), *Urtica dioica* (o.), *Veronica chamaedrys* (o.), together with the tolerants *Pteridium* (o.-l.f.), *Oxalis* (o.), *Luzula pilosa* (o.), and the acidiphilous species *Holcus mollis* (o.), *Potentilla erecta* (o.) and *P. sterilis* (o.). Unfortunately no intensive study of what appears to be a critical example throwing light on the early history of some existing woods has been made, but although the spatial relationships of the different trees have not been examined in detail the structure suggests a developing (ash-)oakwood in which beech has set foot and been maintained in a juvenile state by coppicing. What is known of the early history of Hillocks Wood and its structure leaves little room for doubt that it is essentially a natural though slightly modified development from developing oakwood.

The beechwoods (A_0, *A, B and C*).

In theory the Chiltern beechwoods are managed on the selection system, whereby all age classes of beech ought to be well represented. In fact, the younger age classes are represented by far too few individuals and the older age classes preponderate. The beechwoods thus have the general appearance of even-aged woods with a relatively mature subsidiary vegetation. The

Hampden woods are carefully managed on a system whereby groups or compartments are selectively felled every seven years. Thus, in the change over from a policy of under-felling to one of heavier felling, the number of trees and the condition of the subsidiary vegetation will vary according to the year of the last felling. Younger even-aged groups are also occasionally found, with corresponding effects on the ground vegetation. But on the whole the Chiltern woods may be regarded as mature with mature structure and a full complement of species.

For the characterisation of the beechwoods in seres A_0, A, B and C respectively 1, 10, 7 and 5 examples have been examined. In a general way their distribution on the plateau follows that for the seres as a whole, with seres A_0 (confined to Ashridge) and A next the escarpment, C remote from it and B intermediate. There are, however, exceptions, and topographic variation does not appear to account for all cases. In comparing the seres it should be borne in mind that the one example of A_0 is of small extent with an immature subsidiary vegetation. Furthermore, many beeches have large crowns casting a heavy shade, and altogether this wood approximates to a late associes stage.

Out of 28 phanerophytes there are 4, 25, 20 and 10 in the respective seres. The beech is dominant throughout, and from the magnificent trees of A_0 (*vide* Table III, p. 483) its height and girth decrease to the poor growth found in C. At the same time the number of dominants and the total number of stems increase. The age of the trees in sere C appears to be rather less, but the slow growth makes the counting of rings in the field difficult, and the figures are probably too low—certainly on the low rather than on the high side. The beech is accompanied by oak (*Quercus robur*)[1] in all seres and in all examples of each sere, with a frequency varying from occasional to locally abundant and a height comparable with that of beech, except in C, where the crowns of many oaks project beyond the beech canopy. In the table the figures for the height of the oaks in C were not obtained from selected or dominant trees only, except in one example where the dominant oaks averaged 65 ft. with a girth of 3 ft. 6 in., as compared with 59 ft. and 2 ft. 5½ in. for beech. In the other seres only dominants were measured. It would thus appear from these data that in C oak has a relative advantage. Ash is practically confined to A_0 and A; planted in gaps in B woods it survives to the sapling stage but looks unhappy, in marked contrast to its healthful and vigorous appearance in A_0 and A where mature trees attain the height of the neighbouring beeches. It has a frequency seldom more than occasional but is never absent. *Prunus avium* has a similar but slightly lower frequency in all but one of the A and B woods; as seedlings and young plants it is rare in C, where it has no place in the canopy. In contrast to the native oak, ash and gean the exotic *Acer pseudoplatanus* appears still to be finding its way, for it has a low constancy (2) in A and B but is locally dominant in Cowleaze

[1] *Quercus sessiliflora* is recorded from one wood only, the hybrid from two (both B).

Wood (A), reaching 80 ft. *Carpinus* (A and B) is occasional in one wood and local in two others: *Sorbus aria* (also A and B only) is rare to local.

Table III. *Beechwoods of seres A_0, A, B and C.*

Number and kinds of trees per 10,000 sq. ft. (=0·23 acre), distribution in crown classes, age, height, and girth at 4 ft. 3 in. of the "dominants." (Measurements are in feet and inches.)

Sere	A_0	A					B			C				
Name of Wood or locality	Ashridge	Barnes Grove	Pulpit plateau	Kingsfield (slope)	Kingsfield (plateau)	Sergeant's Wood	Hampden Coppice (plateau)	Keepershill (plateau)	Monkton (part)	Monkton (part)	Monkton (part)	Lodge Wood	Hampden Coppice (slope)	Keepershill (slope)
Av. height of dominant *Fagus*	107	83	81	77	74	70	73	69	70	62·5	59	60	59	56
Av. girth of dominant *Fagus*	5′ 4½″	3′ 8½″	4′ 3″	3′ 8″	3′ 5″	3′ 1″	3′ 3″	3′ 0″	2′ 11″	2′ 7½″	2′ 3″	2′ 6½″	2′ 5½″	—
Approx. age of *Fagus*	145	130	130	140	135	—	135	131	—	125	116	105–140	132	138
Av. height of *Quercus robur*	—	77	74	75	73	—	75·5	—	—	62	—	59	65	—
Av. height of *Fraxinus*	107	77·5	78	78	—	—	—	—	—	—	—	—	—	—
No. of dominant *Fagus*	15	18	18	22	27	26	No plots recorded	39	27	45	51	24	No plots recorded	
No. of subdominant *Fagus*	5	15	1	8	7	19		10	20	31	20	27		
No. of suppressed *Fagus*	—	10	—	8	7	4		4	5	15	24	33		
No. of dominant *Quercus robur*	—	1	—	2	4	—		—	—	—	3	5		
No. of subdominant *Quercus robur*	—	1	—	—	—	—		—	—	—	—	—		
No. of dominant *Fraxinus*	—	—	—	1	—	1		—	—	—	—	—		
Total no. of stems	20	45	19	41	45	50		53	52	91	98	89		

A true shrub layer is quite absent: its potential constituents all have a low frequency and mostly a low constancy. The only shrub recorded from A_0 is *Sambucus*, which is found also in A and B. *Acer campestre* (marginal only), *Pyrus malus* (r.), *Taxus* (occasional in one wood only) are confined to A; *Corylus*, *Rosa arvensis* (constancy 5 in A and 1 in B), *Sorbus aucuparia*, and *Viburnum opulus* (local only) are confined to A and B; *Crataegus* with constancy 4 in B and *Salix caprea* are found in A, B and C, while *Salix aurita* is recorded from a gap in C. *Ilex*, however, has the highest constancy in A, B and C and an average frequency of 2·1–2·2; in gaps it grows to a height of 20 ft. in B and 8 ft. in C, while as a low semi-procumbent bush it is found in all three seres but most conspicuously in C and in particular in Lodge Wood, where it is locally dominant, forming low thickets in which beech leaves collect to considerable depths.

In seres A and B the place of a true shrub layer is taken by *Rubus fruticosus*: in A_0 and C there is no comparable layer. In the immature wood of A_0, *Rubus* is occasional, with a higher frequency at the margin only. Whether it will extend to form a continuous layer cannot be settled in the absence of precise information about the conditions affecting the spread of *Rubus*, in particular its relation to the field layer. Although *Rubus* appears unable to become dominant in the oakwoods of A_0, it does not follow that it will not do so in the beechwood. Here I regard it as potentially dominant. In A and B it forms a more or less continuous layer, broken where the shade is deeper and forming impassable thickets in open woods and in gaps, particularly in A woods. In A its average height varies from 18 to 24 in., in gaps to 4 ft.; in B, 15 to 18 in., and about 24 in. in gaps. It is present in all the examples of C but under canopy it remains an isolated puny plant; in gaps it may, however, become locally dominant, suggesting that in more open but sheltered woods it may even here form a continuous though open layer. *Rubus idaeus*, with constancy 4 in A and B and 2 in C, is local only in all three seres. *Lonicera* for the most part remains a ground plant with the highest constancy in A and B but with a low frequency (1·7) in both; in C it is marginal only in two woods, but like *Rubus fruticosus* it may spread when opportunity offers by the opening out of the canopy.

The effect of this double canopy of beech and bramble is seen in the discontinuity of the field layer, where few species have more than a high local frequency and where the place of most among the significant species is due to a high constancy. This is true of *Oxalis*, though in less degree than for any other species: the woodsorrel has the highest constancy of any herb and a relatively high average frequency in A, B and C. Its frequency varies much in all three seres, from occasional to locally dominant, but on the whole it has higher values (2·9) in A and B than in C (2·3). Its varying frequency is related to the soil (for it is absent from Lodge Wood (C), and generally where the surface soil is compact) and to the shade, for it is locally dominant only under the shade of even-aged groups of relatively young trees where *Rubus* is an occasional and small plant, and occasional to frequent in the older and more open neighbourhood where *Rubus* is abundant to dominant. In this distribution we have clear indications of an *Oxalis* stage followed by a *Rubus* stage in seres A and B, but owing to the system of management this sequence is unable to find expression over whole woods. It may be noted here that even where *Oxalis* does occur in almost pure patches the carpet has not the same continuity as in the plateau woods of the South Downs, except in the flinty Sergeant's Wood where the chalk is near the surface (at 2 ft.), but woodsorrel grows in vigorous tufts, suggesting that the plant experiences certain difficulties in vegetative reproduction, particularly in the thinned portions of C woods.

Thus the shade of beech alone or of beech *plus* bramble prevents the free spread of herbs and grasses and the formation of a field layer in which competition between the different life forms can take place. The differences in floristic composition of the beechwoods will thus be an expression of soil differences within the limits imposed by shade.

In number of species—apart from A_0 with 11—there is a decrease from A to C—75, 56, 51 respectively. The numbers exclusive to each and to the various combination of seres are given in Table IV, distributed in life-form classes. Among herbs and grasses 29 species are found in all three seres, 9 are exclusive to A and B, 12 to B and C, 4 to A and C and 33, 5 and 6 are exclusive to A, B and C respectively. The 29 common to A, B and C, include exacting species (e.g. *Epilobium angustifolium, Dactylis glomerata, Poa trivialis, Milium effusum, Epilobium montanum* and *Circaea lutetiana*—the last two local only in B and C) and the acidiphilous species *Conopodium denudatum, Holcus mollis* and *Rumex acetosella.* All the 33 species confined to A are exacting, with the exception of *Potentilla sterilis* and *Pyrola minor*, while the following acidiphilous species are found in the seres added in parentheses: *Blechnum spicant, Digitalis purpurea, Scilla non-scripta, Stellaria holostea* (A, B), *Anthoxanthum odoratum, Calluna vulgaris, Galium saxatile, Hypericum pulchrum* (B, C), *Hypericum humifusum, Sieglingia decumbens* (B), *Carex pallescens, C. pilulifera, Deschampsia flexuosa, Stellaria uliginosa* and *Juncus bufonius* (C).

The significant species (for A, B and C only) with constancy 4 and 5 and average frequency 2·1 and over, including species with high frequency in gaps, are listed on p. 486. Group (1) includes those significant in the three seres: in group (2) the species are arranged in life-form classes. *Epilobium angustifolium* is included in the list of species common to all three, for although it is confined to gaps in B and C it is largely local also in A. The same holds good for *Juncus communis* which is found almost exclusively in the wetter hollows.

In A_0, half the ground is bare. The most important species is *Mercurialis perennis*, which is locally dominant: it is absent from B and C and local only (often marginal) in A. The other significant species in A_0 are *Athyrium filix-foemina* (o.), *Dryopteris filix-mas* (o.), *Epilobium angustifolium* (l.), *Lastrea dilatata* (o.), *Lysimachia nemorum* (o., marginal), *Oxalis acetosella* (o., marginal), *Pteridium aquilinum* (l.f., marginal), *Urtica dioica* (l.f.) and *Viola silvatica* (o.).

The list of species brings out more clearly the floristic differences separating the seres. It will be observed how in each life-form class or subclass the exacting species head the list and characterise A: markedly acidiphilous species characterise C.

The distribution in the beechwoods of *Holcus mollis* and *Scilla* is chiefly on the margins, where each may be locally dominant: these two species are not normally found scattered through the woods, the heavy shade of the double canopy of beech and bramble probably accounting for their exclusion. High frequency is often correlated with a canopy of mixed oak and beech and with exposed margins where the bramble is less vigorous than in the sheltered parts of the woods. Wood soft-grass and bluebell are essentially relicts from the oakwoods.

Gradation in soil quality is also brought out by reference to the mosses, which have little chance of attaining high frequency except where, as on exposed wood margins, the litter is blown away or the moss shoots are tall enough (*Polytrichum formosum*) to grow through it. *Eurhynchium striatum, Fissidens taxifolius, Mnium rostratum, M. undulatum,* are confined to A, *Webera nutans*

Significant species in the beechwoods of seres A, B and C.

Seres in which the species is significant	Life form	Number of examples ...	Sere A 10		Sere B 7		Sere C 5	
			C.	A.F.	C.	A.F.	C.	A.F.
Group (1). Species with significant values in all three seres.								
A, B, C	P.	Fagus silvatica	5	5·0	5	5·0	5	5·0
A, B, C	P.	Quercus robur	5	2·5	5	2·6	5	2·6
A, B, C	P.	Ilex aquifolium	5	2·1	5	2·1	5	2·2
A, B, C	H.r.	Oxalis acetosella	5	2·9	5	2·9	4	2·3
A, B, C	H.s. (G.r.)	Epilobium angustifolium	3	1·8 l.	4	1·8 l.	3	2·0 l.
A, B, C	H.s.	Rubus fruticosus (agg.)	5	4·6	5	4·7	5	2·0
A, B, C	H.c.	Carex remota	5	1·6	4	1·6	4	2·3
A, B, C	H.c.	Deschampsia caespitosa	5	2·7	5	2·4	5	2·0
A, B, C	H.c.	Juncus communis	3	1·2 l.	4	1·2 l.	4	1·8 l.
A, B, C	H.c.	Luzula pilosa	5	1·7	5	2·0	5	2·2
A, B, C	G.r.	Pteridium aquilinum	4	1·6	5	2·2	5	1·8
Group (2). Species with significant values in one or two seres.								
A	P.	Fraxinus excelsior	5	2·2	2	1·5	—	—
A	P.	Acer pseudoplatanus	2	2·3	2	2·0	—	—
A	P.	Rosa arvensis	5	1·6	1	1·0	Seedling	
A, B	P.	Prunus avium	5	1·9	5	1·6	3	1·0
A, B	P.	Lonicera periclymenum	5	1·7	5	1·7	2	1·0 l.
B	P.	Crataegus monogyna	2	1·8	4	1·4	1	1·0
A	Ch.	Lamium galeobdolon	4	2·1	—	—	—	—
A	Ch.	Euphorbia amygdaloides	4	1·7	—	—	—	—
A	Ch.	Veronica montana	4	1·8	1	1·0 l.	—	—
A	Ch.	Stellaria holostea	4	1·7	1	1·0 l.	—	—
C	Ch. (H.s., G.rad.)	Rumex acetosella	1	1·0 l.	2	1·0 l.	1	3·0 l.
C	Ch.	Calluna vulgaris	—	—	1	2·0 l.	5	1·2 l.
C	Ch.	Deschampsia flexuosa	—	—	—	—	1	3·0 l.
A	H.r.	Viola silvatica	5	2·2	3	1·8	1	1·0 l.
A, B	H.r.	Dryopteris filix-mas	5	2·1	4	1·8	1	1·0
A	H.s.	Geum urbanum	5	1·6	—	—	—	—
A	H.s.	Ranunculus ficaria	2	4·0 l.	—	—	—	—
A	H.s.	Epilobium montanum	4	1·6	1	1·0 l.	1	1·0 l.
A, B	H.s.	Rubus idaeus	4	1·7 l.	4	1·2 l.	2	1·0 l.
B	H.s.	Digitalis purpurea	1	2·0	5	2·2	—	—
C	H.s.	Hypericum pulchrum	—	—	3	1·7	4	2·0 l.
A, B	H.c.	Carex silvatica	5	2·0	4	1·2	1	2·0
A, B	H.c.	Milium effusum	5	2·0	5	1·9	3	1·3 l.
B	H.c.	Festuca ovina	—	—	1	3·0 l.	3	2·0 l.
B, C	H.c.	Holcus lanatus	3	1·2	4	2·0	4	2·0
B, C	H.c.	Agrostis vulgaris	1	1·0 l.	5	1·9	5	2·0
C	H.c.	A. alba	1	1·0 l.	1	2·0	1	3·0 l.
C	H.c.	Anthoxanthum odoratum	—	—	2	1·5	4	2·0 l.
C	H.c.	Carex pilulifera	—	—	—	—	1	3·0 l.
A	G.r.	Asperula odorata	5	2·7	—	—	—	—
A	G.r.	Helleborine latifolia	4	1·9	—	—	—	—
A	G.r.	Anemone nemorosa	2	2·4	—	—	—	—
A	G.r.	Melica uniflora	4	2·0	3	1·3	1	—
A	G.r.	Circaea lutetiana	5	2·1	3	1·0 l.	3	1·0 l.
B, C	G.r.	Holcus mollis	3	1·8 l.	4	2·7 l.	5	2·2 l.
A	G.b.	Scilla non-scripta	4	2·1	1	1·0 l.	—	—
A	T.	Galium aparine	2	2·3	—	—	Seedling	
A	T.	Geranium robertianum	5	2·2	1	1·0 l.	—	—
C	T.	Poa annua	1	1·5	2	1·0 l.	4	1·3 l.
Group (3). Bryophytes.								
A, B, C	—	Polytrichum formosum	5	2·0	5	2·4	5	3·3
A, B, C	—	Dicranella heteromalla	4	1·8	5	2·2	5	2·2
A, B, C	—	Eurhynchium myosuroides	4	2·0	4	2·0	5	2·5
A, B, C	—	Hypnum cupressiforme	4	2·0	4	2·0	5	2·0
A, B, C	—	Mnium hornum	4	2·0	5	2·1	5	3·0
A	—	Eurhynchium praelongum	4	2·0	2	2·0	2	2·0
B, C	—	Dicranum scoparium	2	2·0	4	2·1	5	3·0
C	—	Thuidium tamariscinum	3	1·8	3	2·0	4	2·1
C	—	Hylocomium loreum	1	1·0	1	1·0	4	1·3
C	—	Diplophyllum albicans	—	—	—	—	4	2·0
C	—	Lepidozia reptans	—	—	—	—	4	2·0

to B, *Leucobryum glaucum* to B and C, and *Cephalozia bicuspidata*, *Frullania tamarisci*, and *Hypnum schreberi* to C. All these have low values. Of the 27 bryophytes, 20, 16, 18 are found in A, B and C respectively and include 11 common to all three. The species with high constancy and average frequency values are listed on p. 486 as group (3). The first five on the list are regarded as significant in all three seres and, although the average values differ little, there is a general increase from A to C, and particularly in C where on wind-swept areas *Mnium hornum* is dominant. In A the local abundance of *Polytrichum formosum* is commonly associated with a compact soil.

The bryophytes on the beech stems have not been recorded, but their restriction to the bases of the stems is striking: only rarely do they ascend several feet.

In the spectra (below) of all species and among those common to the seres A, B and C the caespitose hemicryptophytes predominate (Table IV) and weight the values in the separate seres in proportion to the numbers in the seres. This preponderance is nearly overcome in A where the exacting scapose hemicryptophytes bring the numbers almost to parity. In B the caespitose hemicryptophytes definitely lead, with a further relative increase in C. Among rosette hemicryptophytes and rhizome geophytes the numbers common to A, B and C almost account for the totals in B and C, but those exclusive to A bring the numbers up, although the percentage difference is small, and may (in the rhizome geophytes) reverse the numerical relation.

Table IV. *Beechwoods of seres A, B and C.*

Distribution of all species in life form classes exclusive to the various seres and combinations of seres (A, B and C only).

Sere	P.	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	G.rad.	T.	Total
A, B, C	9	3	5	5	12	4	1	2	1	42
A, B	9	2	1	3	0	0	1	0	2	18
B, C	0	2	1	3	5	1	0	0	0	12
A, C	0	0	0	1	1	1	0	0	0	3
A	7	4	6	10	7	3	1	0	2	40
B	2	0	0	1	2	0	0	0	2	7
C	1	1	0	2	2	0	0	0	1	7
Total	28	12	13	25	29	9	3	2	8	129

Biological spectra of all species (seres A_0, A, B and C).

Sere	P.	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	G.rad.	T.	Total
(1) Including phanerophytes.										
A_0	25 (4)	6·25 (1)	31·25 (5)	25 (4)	0	12·5 (2)	0	0	0	100 (16)
A	24·5 (25)	8·5 (9)	11·5 (12)	18·5 (19)	19·5 (20)	7·5 (8)	3 (3)	2 (2)	5 (5)	100 (103)
B	25 (20)	9 (7)	9 (7)	15 (12)	24 (19)	6·5 (5)	2·5 (2)	2·5 (2)	6·5 (5)	100 (79)
C	15·5 (10)	9·5 (6)	9·5 (6)	17·25 (11)	31·25 (20)	9·5 (6)	1·5 (1)	3 (2)	3 (2)	100 (64)
(2) Without phanerophytes.										
A_0	—	8·5	41·5	33·5	0	16·5	0	0	0	100
A	—	11·5	15·5	24·25	25·5	10·25	4	2·5	6·5	100
B	—	11·75	11·75	20·5	32	8·5	3·5	3·5	8·5	100
C	—	11	11	20·5	37	11	2	3·75	3·75	100

Biological spectra of significant species (seres A, B and C only).

Sere	P.	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	G.rad.	T.	Total
				(1) Including phanerophytes.						
A	21·5 (8)	11 (4)	8 (3)	16·25 (6)	16·25 (6)	19 (7)	2·5 (1)	0	5·5 (2)	100 (37)
B	25 (6)	0	8·5 (2)	17 (4)	37 (9)	12·5 (3)	0	0	0	100 (24)
C	12 (3)	12 (3)	4 (1)	16 (4)	36 (9)	12 (3)	0	4 (1)	4 (1)	100 (25)
				(2) Without phanerophytes.						
A	—	14	10·5	20·5	20·5	24	3·5	0	7	100
B	—	0	11	22·5	50	16·5	0	0	0	100
C	—	13·75	4·5	18	41	13·75	0	4·5	4·5	100

These points are emphasised in the spectra of significant species above, but the relation between the scapose and caespitose hemicryptophytes in B and C is the same, while the rosette hemicryptophyte *Oxalis* is the only one represented in C, and *Epilobium angustifolium* and *Pteridium*, common to all three seres, account for the rhizome geophytes, except *Holcus mollis*, in B and C. The bulk of the geophytes are confined to A. Chamaephytes are absent from B: they are exclusive to A and C, with different species in the two. *Scilla* is the only representative of the bulbous geophytes and it is confined to A, while *Rumex acetosella* and *Poa annua* represent the root-bud geophytes and the annuals respectively in C. The exacting annuals *Galium aparine* and *Geranium robertianum* are confined to A.

The bramble layer has an important effect on the regeneration of the dominant trees. Beech sets seed and produces seedlings freely in A, B and C—there are no observations from A_0—and after the mast year in 1922 the ground in C was carpeted with seedlings, some of which still survive. In C, however, they do not have to contend with brambles. The effect of the bramble is well illustrated by an experiment carried out some years ago by Mr Hobart-Hampden in a B wood where the bramble was cut and kept cut for some years on two strips. The adjoining uncut bramble served as a control. In 1926, when I saw the experiment, there were no young beeches among the uncut bramble, but a number survived on the cut plots. The experiment further demonstrates the effect of rabbits (or hares), for one cut and one uncut strip were enclosed by wire netting, the other cut and unprotected strip serving as a control. More beeches survived inside the enclosure than outside: they were also taller because those outside had been nibbled by rabbits. The difficulties of beech regeneration are increased in A and especially in gaps, where the tangled thickets of *Rubus* render survival of the seedlings impossible. In smaller gaps occasional young beeches are found where the *Rubus* is not so dense. Oak does not regenerate freely: it is represented by occasional seedlings and saplings only. Of the three important trees in A, ash reproduces most freely: ash and probably also oak have the power of growing through the bramble cover where beech fails, thicket ash growing up and suppressing the brambles. This differentiation is very important for it ensures the constant presence of ash and oak in the beechwoods of A and of oak in the beechwoods of B, and at the same time the maintenance of beech because under the canopy of oak and ash beech can grow up. Thus by encouraging ash and oak the beechwoods themselves can be maintained without incurring the expense of cutting the brambles to ensure the survival of the beech. The mixture is also desirable from the soil point of view (see p. 494). Special reference is made later to *Acer pseudo-platanus* which is dominant in part of Cowleaze Wood, and although no observations enable me to assert that it penetrates a bramble cover it is probable that it can do so.

CHANGES IN THE FLORISTIC CORTÈGE AND IN THE CONSTANCY AND FREQUENCY OF CERTAIN SPECIES DURING SERAL DEVELOPMENT.

The rise to dominance of the oak and its fall before the beech brings in its train changes in the floristic cortège. Oddly enough, the number of species in the several woodland stages of sere A (the only sere where the number of examples is comparable) is remarkably constant, except in the beech associes with a 33 per cent. drop. In this sere there are 143 species (42 woody plants and 101 herbs). Of the species found exclusively in developing woodland, oakwood, beech associes, and beechwood respectively, in any combination of two, three or all four, by far the largest number, substantially more than a third of the whole (15 woody plants and 40 herbs), are common to all four stages.

Dealing first with woody species and, as with herbs, making allowance for what appears to be fortuitous distribution, we find an early disappearance of the shrubs (*Crataegus monogyna*, *Prunus domestica*, *Rosa canina* and *Ulex europaeus*) associated with the developing woodland. *Cornus sanguinea*, *Ligustrum vulgare*, *Rosa dumetorum*, *Solanum dulcamara* and *Tamus communis* survive to the oakwood stage but are absent from the later stages; *Prunus spinosa*, to the beech associes, while the denser shade of the same community excludes *Acer campestre*, *Carpinus betulus*, *Salix caprea* and *Sorbus aria*, which are found in the other three.

Of the 15 woody species common to all, some show a regular change in constancy and average frequency. *Fagus*, of course, with the highest constancy in all stages increases its frequency and the only other species to follow a parallel course (apart from a deviation with reduced frequency in the beech associes) is *Rubus fruticosus*. Ash attains its maximum frequency in the developing woodland and thereafter maintains itself with high constancy, except in the associes, but with a much reduced frequency. Oak, with constancy 5 in all, is naturally dominant in the oakwood, its frequency rising and falling with a gentle gradient before and after respectively. Both *Corylus avellana* (with high constancy and high frequency) and *Viburnum opulus* (with high constancy) are essentially oakwood species. *Lonicera periclymenum* too is closely associated with oak, for it maintains a high frequency so long as oak is an important constituent in the canopy but its numbers drop suddenly in the beechwoods, though it maintains a constancy of 5 throughout. *Ilex* *aquifolium*, on the other hand, is not characteristic of any particular stage, for it has a high constancy and a relatively low frequency in all. *Crataegus monogyna*, by its presence throughout the sere shows a greater power of enduring shade than *Prunus spinosa*, but drops suddenly in numbers with a gentler fall in constancy, whilst *Sambucus nigra* drops abruptly in constancy but has a low frequency throughout. *Rosa arvensis* and *Prunus avium* (except in the oakwood) show no important change, maintaining a high constancy and a low frequency. *No tree or shrub makes its first appearance either in the beech associes or in the beechwood.*

As the grassland of the commons covers a wider range of soils than sere A, strict comparison is not justified, but it may be mentioned that all the species named above (except *Ligustrum*) are found on the open common. Among the species which show a change in frequency or constancy as the result of succession to woodland, the most important, besides ash, oak and beech, are *Corylus*, *Lonicera*, *Rubus* with increased frequency and *Ilex* and *Viburnum* with increased constancy.

The dense canopy formed during the slow development of the developing woodland explains the abrupt change from the heliophilous flora of grassland to the shade flora of the woods. But, where bracken is dominant, the change has already begun by the exclusion of some grassland species and the encouragement of facultative shade plants, notably *Holcus mollis*. Among the more important species significant on the commons as a whole and persisting throughout the sere are *Agrostis vulgaris*, *Dactylis glomerata*, *Deschampsia caespitosa*, *Digitalis purpurea*, *Epilobium angustifolium*, *Holcus lanatus*, *H. mollis*, *Poa trivialis*, *Pteridium aquilinum*, *Veronica officinalis*, *Potentilla sterilis* and *Veronica chamaedrys*—the last two absent from the beech associes. Others survive to different stages; *Campanula rotundifolia* (a species significant in the sanicle beechwood of the escarpment, yet absent from all plateau beechwoods), *Clinopodium vulgare*, *Rumex acetosa* to the developing woodland: *Anthoxanthum*, *Cirsium palustre*, *Prunella vulgaris* to oakwood; and *Galium saxatile*, *Poa pratensis*, *Potentilla erecta* and *Ranunculus repens* to the associes.

Among the 40 species found in all four stages of the sere some persist without important change in their constancy and frequency values. *Agrostis alba*, *Asperula odorata*, *Athyrium filix-foemina*, *Bromus asper* (marginal and local only in the beechwood), *Dactylis*, *Epilobium angustifolium*, *Galium aparine*, *Holcus lanatus*, *Lysimachia nemorum* and *Veronica officinalis*: with reduced values in the associes occur *Circaea*, *Deschampsia caespitosa*, *Fragaria vesca* and *Viola silvatica*. In the developing woodland values are higher for *Arenaria trinervia*, *Brachypodium silvaticum*, *Digitalis*—all with higher constancy: in the oakwood for *Holcus mollis*, *Scilla non-scripta*, *Pteridium*—generally with a higher frequency, and *Mercurialis perennis* (largely local): in the associes with a high constancy *Agrostis vulgaris* and in the beechwood *Carex remota*, *Epilobium montanum*, *Melica uniflora*, *Milium effusum* (with higher frequency in the associes), *Stellaria holostea* and *Veronica montana*—all with higher constancy values. The following species show a gradual decrease in values: in constancy, *Digitalis*, *Poa trivialis*, *Primula vulgaris*; and in frequency *Lamium galeobdolon*, *Nepeta* and *Sanicula europaea*. *Oxalis* and *Deschampsia* show a gradual increase in frequency and *Dryopteris* in constancy.

Some species make their first appearance in stages later than the developing woodland and persist to the beechwood: *Anemone*, *Blechnum*, *Euphorbia amygdaloides* and *Luzula pilosa* in the oakwood; *Monotropa* and *Pyrola minor* in the associes, while *Carex strigosa*, *Lactuca muralis*, *Ranunculus auricomus* and *Rumex acetosella* are recorded only from the beechwood.

In sere B, where oakwoods and beechwoods only can be compared, the following woody plants, apart from oak and beech, show significant changes: *Corylus* with a higher constancy and frequency, and *Lonicera* with a higher frequency in oakwoods, *Prunus avium* and *Rubus idaeus* with higher constancy in beechwoods, while *Rubus fruticosus* maintains high values in both. *Agrostis vulgaris* and *Holcus mollis* show similar values in the two stages. *Carex remota*, *C. silvatica*, *Digitalis*, *Epilobium angustifolium*, *Luzula pilosa* have increased constancy values in the beechwoods, *Deschampsia caespitosa* increased constancy and frequency, while *Oxalis* has a higher frequency. On the other hand *Anthoxanthum* and *Pteridium* decrease in frequency, while the following are found in the beechwoods only, *Athyrium filix-foemina*, *Dryopteris filix-mas*, *Lastrea dilatata*, *Milium effusum*, *Monotropa* and *Rumex acetosella*. Let it be noted that while the three ferns occur in all stages of seres A_0 and A, they are confined to the beechwoods of seres B and C, being absent both from the oakwoods of B and the mixed associes of B + C.

The analysis makes it obvious that the clear-cut distinctions normally found between oakwood and beechwood do not hold here. Tendencies are clear enough, especially in the oakwood of A with *Lonicera*, *Holcus mollis*, *Pteridium* and *Scilla*, but the sharpness of the break due to a change in light intensity is obliterated. The devil in the piece is the bramble and its machinations would be more far-reaching if the oakwoods were mature. It is also clear that apart from the presence of exclusive species like *Monotropa* and the altered values of constancy and frequency due to modifications in the internal climate of the beechwoods, the floristic cortège is fundamentally the property of the sere, determined by soil and not the specific property of beechwoods.

CHANGE IN THE BIOLOGICAL SPECTRA OF ALL SPECIES EXCEPT PHANEROPHYTES DURING THE SUCCESSION IN SERES A AND B.

Monotropa in the beech associes of A and *Monotropa* and *Rumex acetosella* in the beechwoods of A and B account for the representation of root-bud geophytes in the later stages of the succession only.

From sere A_0 to C, in the seres as a whole or in the beechwoods only, the most significant feature is the changing relation between the scapose and caespitose hemicryptophytes: as the scapose hemicryptophytes dwindle in importance the caespitose hemicryptophytes rise. This is repeated in the spectra of the seral stages of A but the differences are scarcely significant except in the developing oakwood with more scapose hemicryptophytes and in the beech associes with more caespitose hemicryptophytes. In the oakwoods of B the two life-forms are numerically equal, but in the beechwoods the caespitose are higher by 11·5. It would thus appear that in the beechwoods the caespitose are favoured relatively to the scapose forms.

Taken by themselves these data cannot be unduly stressed, for the number of examples is small and more important still the assignment of the different examples to their respective seres is based on floristic and vegetational likeness and not on essential identity of the habitats. The differences therefore may quite well come within the range of variability in the sere. Furthermore the basis of assignment in part at least excludes the identification of a change due to beech. For example, a major change equal to the difference between the seres would automatically result in the assignment of the beechwood example to the next sere. These disqualifications are removed in the analysis of the woodland vegetation of seres 2 and 3 of the South Downs plateau where we can be reasonably certain of the essential identity of the habitats in the ash-oakwood and the beechwood of the respective seres. Yet the same change is noted in the relation between the scapose and the caespitose hemicryptophytes: in the ash-oakwoods (seres 2+3) there are 39 per cent. scapose and 12 per cent. caespitose hemicryptophytes: in the beechwoods of the same seres 16·5 and 23·5 per cent. respectively.

The same differences are noted between the Herbaceous Beechwood (Scottish) on the one hand and the Heath Beechwoods of northern Scotland and southern England on the other (8).

Thus there is some evidence to show that the differences in the spectra due to habitat differences are paralleled within the sere by the influence of the beech: that in short there may be an edaphic succession caused by beech.

THE EFFECT OF BEECH ON THE SOIL.

A comparison of the pH and the distribution of the organic matter in the surface soil layers of the beechwoods of seres A_0 to C cannot provide evidence which will throw light on this problem, but the data given below show the kind of change to expect at any given point in the series: to these are added data from seres 1, 2 and 3 of the South Downs plateau.

The data show a gradual reduction in organic matter, both in the total amount at the surface and in the differences between the amount at the surface and at 3 to 6 in., from the extremes towards the middle. Further, as already pointed out, burrowing animals like mice and moles are typically absent from C and present in A_0, A and B. This discrimination may be primarily edaphic and have nothing to do with beech, since animals are absent from the soil, and symptoms of podsolisation are present under oak and *Calluna* (Naphill) with no evidence to prove that they are caused by either. Now the removal of the surface peaty humus in C reveals a reticulum of canals, the abandoned and caved-in burrows of mice, and the same observation has been made in the soil below a pioneer beech growing just outside a B beechwood and standing near a pioneer ash (with *Rubus* and *Asperula* below), under which the soil is honeycombed with burrows. In fact within a short distance of each other seres A, B and C are represented. Soil variation is suspected but this cannot explain the abandonment by animals of the area under the pioneer beech, and probably does not explain the accumulation of peaty humus and the initiation of a podsol profile in C beechwoods.

The height (in feet) of mature beech, the pH *of the surface* 6 *in. and the distribution of organic matter in the surface soil layers of beechwoods on the South Downs and Chiltern plateaux.*

	South Downs			Chiltern Hills				
Locality	Charlton Forest (sere 3)	Charlton Forest (sere 2)	Singleton Forest (sere 1)	Ashridge (sere A_0)	Hailey Wood (sere A)	Keepers-hill Wood (sere B)	Lodge Wood (sere C)	
Height of mature beech	90	100	107 (by extrapolation)	107	89	69		60
*p*H of surface 6 in.	7·7	5·8	5·1	5·2	4·7	4·6		4·1
Loss on ignition:								
0–1½ in.	16·37	13·16	11·02	8·58	9·57	11·25	Black peat (Trockentorf)	71·72
1½–3 in.	9·01	9·22	7·93		8·31	5·66	Lower part (¼ in.) of black peat	26·36
3–6 in.	9·30	8·00	6·76	7·32	7·72	4·78	Upper ¼ in. bleached horizon	13·22
							¼–1¼ in. bleached horizon	5·72
							1–4 in.	6·09
							4–7 in.	3·97

Now the soil is buffered against acid, yet comparison of the *p*H of the surface layers of soil under beech and under adjoining oak or ash—a method which does not entirely exclude the possibility of soil variation accounting for the differences—gives highly consistent lower values under beech, and these same differences are found in other places (p. 494). Only a selection of the data is given here and in all contrasted sets, except two, one of which is given in the last two columns, the values under beech are lower.

Appeal to the South Downs plateau again shows that not only are the *p*H values very much lower under beech families round beech invaders in the ash-oak associes of sere 3 than under the adjoining ash-oak canopy, but by spring-time scarcely any whole leaves, other than scattered beech leaves, are left on the soil, whereas under beech the beech litter accumulates. From one square foot under ash-oak in April the following weights in grams were obtained: oak leaves 5·5, ash petioles 3·5, beech leaves 1·5 (total weight 10·5). Under beech there were oak leaves 1·8, and beech leaves 37·3 (total weight 39·1). Further, in parts, the beech humus next the soil is blackish in colour. Furthermore, mole hills are scarce or absent from the area occupied by the

Comparison of the pH *values, determined electrometrically*, of the surface soil under beech, and under adjoining ash, oak and birch.*

Locality ...	South Downs plateau					
Tree species ...	Ash-oak	Beech	Mixed coppice	Beechwood	Ash	Beech
Depth of sample (in.):						
0–1½	6·87	4·99	6·47	5·43	6·41	5·45
1½ 3	6·26	5·24	6·39	5·48	6·09	5·42
3 6	5·95	5·09	6·17	5·56	5·74	5·44

Locality ...	Burnham Beeches				Chertsey	
Tree species ...	Oak-beech	Beech	Oak	Beech	Oak-birch	Beech
Depth of sample (in.):						
0–1½	3·91	3·79	4·53	3·85	4·55	3·92
1½–3	3·91	3·77	4·39	4·11	4·15	4·02
3-6	3·91	3·91	4·41	4·37	4·21	4·13

Locality ...	Chiltern plateau					
Tree species ...	Ash	Beech	Ash	Beech	Oak	Beech
Depth of sample (in.):						
0-1½	4·79	4·25	4·73	4·51	4·05	4·38
1½–3	4·74	4·38	4·73	4·49	4·29	4·24
3–6	—	—	4·75	4·57	4·44	4·34

* The soils of seres 1, 2 and 3 on the South Downs plateau and of A_0, A and B on the Chiltern plateau contain much manganese: sere C contains only a little. The results obtained by the quinhydrone method are therefore too high and acceptable as comparative only.

beech and common elsewhere in the wood. The absence of moles' activities as well as the reduced activity of earthworms is reflected in the distribution of the humus. Data from a mixed oak and beech wood on loam in Burnham Beeches show the same phenomenon.

Distribution of organic matter in the surface 6 *in. of soils under beech and under adjoining oak or ash and oak.*

Locality ...	South Downs		Burnham Beeches	
Canopy ...	Ash + oak	Beech	Oak	Beech
Soil layer, 0–1½ in.	14·73	15·71	9·57	14·20
1½–3 in.	12·96	12·09	6·49	6·48
3–6 in.	11·90	9·57	4·42	4·56

There is therefore reasonable ground for the conviction held by British foresters that on certain soils, at least, beech brings about soil degeneration.

The explanation of the problem has engaged the attention of investigators since the publication of Müller's classic (4), but a full discussion of it cannot be entered into here. Suffice it to say that the common occurrence of the phenomenon in western Europe suggests a climatic cause, in particular the soil climate as determined by the beech, directly by the canopy and indirectly by the blanket of litter; but that the soil itself, by determining the Si/Ca ratio in the leaves and hence the rate of decay, is important has been shown by Krauss (3). It may well prove that simple causes are operative and the physical opposition to the activities of animals of a network of roots, particularly of pioneer trees, may be added as a suggestion worth further inquiry.

On the Chiltern plateau the litter of oak and ash decays readily enough, although the shortage of earthworms, particularly in C, is bound to affect the rate of disappearance of oak leaves. Sycamore leaves in sere A decay quickly: by spring most of the autumn fall has disappeared. This is important because the sycamore can take the place of beech in facilitating the production of clean timber without apparently having an adverse effect on the soil. On this last point, however, no analyses have been made.

DISCUSSION OF THE RESULTS.

DOES BEECH FOREST REPRESENT THE CLIMAX COMMUNITY ON THE CHILTERN PLATEAU?

The floristic and vegetational differences between the parallel seres are correlated with differences in the soils. They show a profile of the brown earth type except in C where the distinct, though narrow, A and B horizons denote podsolisation. But the distribution of organic matter both above and in the surface soil layers and the accompanying differences in soil texture reveal a gradient from a typical "mull" soil in A_0 and A, through B where the tendency to form raw humus is present, to C with a marked "Torf" layer. These differences are primarily correlated with soil type. But the absence of calcium carbonate, the low *p*H, exchangeable calcium and basicity all point to potentially infertile soils, although a gradient of fertility from A_0 to C is clear.

This gradient is also indicated by the species found in the different seres. Typical calcicoles are absent, but the restriction of exacting species, like *Fraxinus excelsior*, *Cornus sanguinea*, *Mercurialis perennis* and *Sanicula europaea* to seres A_0 and A and their exclusion, except locally, from B and C afford evidence of such a gradient of fertility: it is further supported by the gradient in vigour of species like oak and beech common to all four seres. At the same time acidiphilous species like *Conopodium denudatum* and *Holcus mollis* are found in all, but some, like *Deschampsia flexuosa*, with more marked preferences, are limited to B and C. This common substratum of acidiphilous species is paralleled by the presence of nitratophilous species like *Epilobium angustifolium* and *Rubus idaeus*, so that deficiency in the nitrifying power of the soil, leaving aside the degree of nitrification, is not the factor or complex of factors which excludes the more exacting species.

The physical properties of the soil also exhibit a gradient and it is possible that it is in the open friable texture of the surface layers and its better aeration, with corresponding reactions upon the availability of the minerals and the ability of the plant to absorb them, that the main factor differentiating A_0 and A from B and C is to be sought. The restriction of *Scilla non-scripta* to A_0 and A finds a parallel in its commoner occurrence in the Dry Oakwood than in the Damp Oakwood and the gradient in vigour of *Pteridium aquilinum* may, in part, be attributed to the same cause. Unsuitable physical conditions appear also to set limits to the spread of *Oxalis acetosella* in C where its local occurrence is closely correlated with the activity of mice in the soil. But how far exacting rhizomic species have their limits determined by chemical insufficiency of the soil in B and C or by its physical unsuitability is not known.

The factor common to all seres is the essential dryness of the habitat, both in atmospheric and soil moisture, safeguarded however against drought by the retentive properties of the soil. The absence of *Erica cinerea* and *Vaccinium myrtillus*, the general restriction of bryophytes to the base of the beech stems, the general scarcity of ferns (except, of course, the bracken), the restriction of *Athyrium filix-foemina*, *Dryopteris filix-mas*, and *Lastrea dilatata* to the beechwoods of B and C and the enhanced vigour of *Rubus fruticosus* in the woods compared with the open commons all point to atmospheric dryness: the general aspect of the vegetation also indicates a soil of mean moisture conditions, or a relatively dry one, except in the patches picked out by *Cardamine flexuosa* (A_0), *Ranunculus ficaria* (A), *Circaea lutetiana* (B and C) and *Juncus communis* in all.

It is this essential dryness over a range of loamy soils which enables the beech to attain dominance and differentiates the series from the extremes of the Damp Oakwood—Dry Oakwood series, where beech is on the whole excluded from the one and potentially dominant in the other. *Pteridium* runs a parallel course but is never dominant in the Chiltern woods. On the loams intermediate between the heavy clay of the Damp Oakwood and the sands of the Dry Oakwood, as on the acid loams of the Reading Beds exposed at Burnham Beeches, mixed oak and beech form woods closely resembling the *Rubus* woods of the Chiltern plateau. And similar tendencies are obvious in mixed oak and beechwoods on loamy sands in Sussex. It thus seems likely that *Rubus* oakwoods do exist or have existed, but that their absence or scarcity is due to the suitability of such soils for arable cultivation. On soils of this nature, somewhere between the extremes indicated, one may look for conditions in which oak and beech would be co-dominant.

In the struggle between oak and beech, *Rubus* tends to tip the balance in favour of oak, as already noted. It also affects the field layer and possibly the shrub layer. Puck is not more mischievous. In A_0 its influence is least, and here, within the limits determined by soil, there is in the oakwoods a potential shrub layer poor in species and in individuals and a continuous field layer, moderately rich in species and rich in individuals, showing a vernal aspect of *Scilla non-scripta* as a striking feature. In the immature oakwood of A the same tendency is noted but the attempt is stifled by the spread of *Rubus*, whose evergreen canopy deepens the shade and reduces the number of individuals, if not of species, in both spring and summer aspects. Aided by the heavier shade of beech the process of exclusion goes further: a spring aspect is absent except near exposed margins where the vigour of *Rubus* is checked and *Anemone* and *Scilla* reveal what might have been. But collectively the woods of A are not floristically poor, although paucity of individuals gives that impression, and so the argument from floristic poverty for the "unnaturalness" of the beechwoods loses its point. The same general features are noted from B woods, floristically poor because of the soil and poor in individuals because of *Rubus*, and in C poorer still in species and in individuals because of the soil alone, aided, however, in exposed examples by the wind. Whether *Rubus* could extend in C on the opening out of the beech canopy is an open question, as it is in the beechwoods of A_0. In the oakwoods of A_0 the failure of *Rubus* to subdue the field layer may be due to the crippling effect of a heavy canopy of herbs on its establishment whether vegetatively or by seed.

Thus the primary distinction between the seres is due to soil differences, in part chemical, in part physical; and the *Rubus* layer in A and B, by altering the character of the field layer, in particular the frequency of the species, is like a wedge driven between A_0 and C, obscuring the relationships in the graduated series A_0, A, B and C.

The data given in the previous section would seem to imply that beech brings about soil degeneration and an edaphic succession from A_0 to C. It may be said at once that there is no evidence to prove that such a far-reaching change has taken place, for the character of the existing woods is correlated with major soil differences. Evidence of secondary change, due to beech, exists in all seres, but the influence of beech in high forest is not so great as in the form of pioneers. Nevertheless it makes for soil degeneration.

The issue is not simple. The present status of the beech may be due to planting, to tipping the balance in favour of beech by cutting out its rivals (ash and oak in A_0 and A, and oak in B and C) so that the natural climax of the succession may not be pure beech at all. But the evidence points to the conclusion that on all the soils described here beech, by outgrowing and suppressing its rivals, forms the major portion of the canopy. Two qualifications must be made: first the influence of *Rubus* tends to maintain a proportion of ash and oak in the canopy of A and of oak in B; and secondly in C a proportion of the oaks grows straighter and taller than beech. The evidence alluded to may be summarised here. Some woods and parts of woods, not described in this paper, clearly have their origin in the natural invasion of land adjoining beechwood: some, like Hillocks Wood, are derived from "scrubs" and are on the way to become beechwood; Monkton beechwood is described in the working plan of the Hampden Estate (1910) as containing many coppiced beech trees, and the developing woodland shows that beech can and does invade ash-oakwood and oakwood. Further evidence from the names of woods points in the same direction: Hampden Coppice and Oaken Grove are beechwoods: High Scrubs, both beechwood and oakwood, probably indicates the change over from coppiced "scrubs" to high forest. And it is quite conceivable that the enclosure at the beginning of last century and the suspension of the practice of coppicing "scrubs" containing few species of trees and much beech led to a rapid change in the aspect of the woods and to the dominance of beech.

On the other hand the scarcity of oakwood is remarkable, all the more so as oak is a constant constituent of beechwoods and is the most successful coloniser of the commons. Further, as Mr Leslie S. Wood informs me, records exist for the Mapledurham Estate near Reading showing that planting on arable land has taken place; and Mr R. Bourne, who has gone into the question more fully than I have, and over a much wider field, informs me that many of the beechwoods have been planted.

These facts point to one of two conclusions: either the climax has been reached over the whole of the plateau or the present regime is partly or wholly artificial—partly if the natural process of succession has been speeded up by the planting of beech and the exploitation of oak and ash, wholly if beech has everywhere been planted wholesale. Not to leave the matter, as Sir Roger would, by saying that "much might be said on both sides," I would express the view that while certain of the beechwoods have undoubtedly been planted, there is also clear evidence in some of them that they have reached their present state by natural development, leaving aside the question whether the trees which provided the seed were planted or not.

But whether the beech has been planted or not the evidence points to the conclusion that beech high forest has not been in existence so very long, perhaps not more than 150–200 years, and since coppicing tends to maintain a high *p*H in the surface soil the beech as a dominant in high forest has not had a very long period during which to make its influence felt on a resistant soil. It seems likely therefore that beech, given unlimited time and an unchanging climate, will bring about a soil change, but will not necessarily yield place to oak, since the change is in a direction which, while it gives oak a relative advantage in height growth, does not exclude beech from dominance. The ultimate fate of the beechwoods would be retrogression to heath. On the other hand (under oak) the soil status would be maintained, as also under hornbeam whose leaves decay quickly.

SOME SUGGESTIONS REGARDING WOODLAND MANAGEMENT.

The exploitation of the beechwoods under the selection system maintains a permanent canopy both of beech and generally of *Rubus* (seres A and B), both of which tend to keep the soil cool. This condition, however advisable in Central Europe, is scarcely a desideratum in our oceanic climate. Soil retrogression is promoted by the maintenance of a low temperature and a high relative humidity, particularly of the soil climate, ensured by the triple cover of beech, bramble and litter. When we add to this the resistance to decay of beech leaves compared with those of ash, oak and sycamore, the beech emerges as the least desirable of the four trees if the maintenance of soil fertility is a crucial question. It is not contended that a marked effect would be produced in a short time by maintaining beech as a pure crop in A_0 and A, but a more generous admixture with ash and oak, both of which grow exceedingly well in these seres, would counteract the evil effects of the beech. They might indeed be obviated entirely by replacing beech with sycamore, which promotes the growth of clean timber in oak and ash and, as far as can be judged from field observations, maintains the fertility of the soil.

The Chiltern soils are essentially hardwood soils: conifers easily succumb to *Armillaria mellea*, although on the Hampden Estate there are small patches of quite good *Larix decidua* (sere A, quality class 2). No information is available concerning the sycamore in B and C, and in any case its best and chief market is for the larger timber that can be grown in A_0 and A. In the circumstances and as long as beech of smaller dimensions is profitable to grow the immediate profits may be diluted by mixing beech with oak for the sake of the soil. In C opening out of the canopy has, according to Mr Hobart-Hampden, produced better growth in the beech.

Selective felling of the beech with a complete disregard of the incidence of full mast years plays into the hands of the bramble, which is a controlling factor and generally remains so under the selection system in woods of seres A and B. By maintaining even-aged groups or whole compartments, regeneration in the *Oxalis* stage, followed by a heavy thinning, secures freedom from competition with the bramble and the light intensity necessary to the survival of seedlings attacked by *Typhlocyba douglasii*.

GENERAL COMPARISON BETWEEN THE WOODY VEGETATION OF THE ESCARPMENT AND THAT OF THE PLATEAU.

Floristically there is not the abrupt change one might expect in passing from the shallow calcareous soils of the escarpment to the deep acid loams of the plateau. While marked calcicoles characterise the sanicle beechwood at the one extreme and equally marked acidiphilous species the beechwoods of sere C at the other, the large body of exacting species found in the sanicle and mercury beechwood and also in seres A_0 and A link the two major groupings—escarpment and plateau—as the less marked acidiphiles link A_0 and A with B and C. Since these exacting species have the same range as ash, and the acidiphiles as oak, they may conveniently be called the ash and oak cortèges respectively.

Apart from sere A_0 there is a gradual reduction in the total number of species from the escarpment to sere C. Among the woody plants of the plateau woods only the more tolerant survive in C, but *Rosa tomentosa* in A_0 and *Salix aurita* in C are not recorded from the escarpment. Among shrubs and dwarf shrubs not associated with woodland, some are exclusive to the plateau:

Calluna vulgaris, *Genista anglica*, *G. tinctoria*, *Sarothamnus scoparius*, and *Ulex europaeus* are the most important. The increasing dilution of the relationship with the escarpment seres, due partly to the elimination of species and partly to the presence of an increasing number not found on the escarpment, is clear from the following data, relating to all herbaceous species, whether purely local or not, expressing the number of escarpment species found in each plateau sere as a percentage of the total found in each sere: A_0, 82·5; A, 72; B, 61; C, 60. If significant and differential species alone are taken, the disparity between A_0 and A on the one hand and B and C on the other would be even greater, owing to the elimination of the ash cortège from B and C. The bryophytes show a similar, though not a continuously weakening relationship: A_0, 100 per cent.; A, 75 per cent.; B, 86 per cent.; C, 73 per cent.

Vegetationally the difference is striking, though it is of course softened by the dominance of the beech throughout. Oak as a significant species is confined to the plateau where it plays an important part in all seres. Ash with high constancy in the juniper sere, high constancy and the potentiality of forming a consocies in the hawthorn sere is limited on the plateau to seres A_0 and A, in both of which it is significant in the seral stages and in the beechwoods. In all three species maximum growth is found in sere A_0. In the succession the juniper scrub is a striking feature of the juniper sere on the escarpment: juniper is scarce on the plateau, playing a negligible part in the succession, and appearing only in (B and) C. Complementary to juniper are hawthorn and blackthorn which form scrub in the intermediate seres (hawthorn in A_0 and A). Like juniper, yew is a feature, though rather local, of the escarpment: on the plateau it is scarce.

Apart from the poor attempts in the oakwoods of A_0 and A, a true shrub layer is absent throughout.

It is the field layer (and the related *Rubus* layer) which presents the greatest contrast. Rich in species and in individuals and continuous in the beechwoods of the escarpment, it is, except in A_0, discontinuous in the plateau woods, where decreasing soil fertility and the *Rubus* layer in A and B increasingly suppress the rich field layer of A_0. Floristically the sanicle and mercury beechwoods are closely allied: vegetationally they differ most obviously in the dominance of mercury in the mercury beechwoods, and it is the important part played by mercury in sere A_0 which binds this sere most closely to the mercury beechwoods of the escarpment. A_0 is differentiated from escarpment woods by the important oak cortège of *Scilla*, *Pteridium*, *Lonicera* and *Holcus mollis*.

The closer kinship of sere A_0 with the mercury beechwood is emphasised by the resemblance between the biological spectra of significant species. Both are characterised by the predominance of scapose hemicryptophytes, and the differences in all life-form classes and subclasses are negligible except in the rhizome geophytes: the mercury beechwoods have 5 per cent., while sere A_0

has 13·5 per cent. *Circaea lutetiana* and *Epilobium angustifolium* are common, while *Asperula odorata, Holcus mollis, Paris quadrifolia* and *Pteridium* are significant in A_0.

GENERAL COMPARISON WITH THE VEGETATION OF THE SOUTH DOWNS.

Sere 4 on the South Downs escarpment and seres 3, 2 and 1 on the plateau form a continuous floristic, vegetational and edaphic series without abrupt change (**8**). Sere 4 closely resembles the sanicle and mercury beechwoods of the Chilterns escarpment but nothing strictly comparable to seres 3 and 2 has been described from the Chilterns, for they contain calcicoles like *Cephalanthera grandiflora* and *Galium mollugo*, not found on the Chiltern plateau. On the other hand sere 1 on the deepest soil, highly acid at the surface, but represented by immature beechwoods only, presents both vegetationally and edaphically the nearest approach to seres A_0 and A and very close to it comes the "beechwood on the plateau" (of the South Downs) described by Adamson (**1**). The scarcity and immaturity of the woods prevents detailed comparison.

Practically all the species from sere 1 and from Adamson's plateau beechwoods are recorded from seres A_0 and A, with the exception of *Hypericum androsaemum, Rubus caesius, Ruscus aculeatus, Viburnum lantana, Eupatorium cannabinum, Hypericum hirsutum, H. perforatum, Inula squarrosa* and *Luzula forsteri*, some of which probably indicate a local approach of the chalk to the surface. Noteworthy absentee trees from the South Downs are *Carpinus betulus* and *Prunus avium* (sparingly present in Adamson's beechwoods). The herbaceous flora is essentially the ash cortège with some tolerants, but in the developing woodland described by Adamson, *Anthoxanthum odoratum, Galium saxatile* and *Hypericum humifusum* of the oak cortège are found. Unfortunately no high forest of oak is available for comparison but already in the ash-oakwoods of seres 3 and 2 there appear *Lonicera, Pteridium* and *Scilla* of the oak cortège, and the larger and marked representation of this element in Adamson's "oak-hazel coppice" (**1**, p. 179) links these woods very closely to the oakwoods of A_0.

Vegetationally the beechwoods of seres 1, A_0 and A are much alike, with the same trees showing vigorous growth, a true shrub layer absent, a *Rubus* layer in sere 1 and A (potential only and long delayed in the life history of the beechwood of A_0) and a discontinuous field layer. But in the oakwoods of the same seres, if one may venture on any comparison between high forest and coppice-with-standards, an important difference lies in the relative development of the shrub layer and the *Rubus* layer. The shrub layer, better developed in A_0 than in A (except locally) is nevertheless poorly developed in both, and poor in species: coppice derived from it must have a uniformity in woody species quite unlike the rich coppice of the South Downs generally and of Adamson's oak-hazel coppice in particular. The soil of the oak-hazel coppice is not uniform and is less acid than in sere 1. But it is possible that with further leaching the ash cortège would become less abundant and the copse consist of fewer woody species. The corresponding high forest with an impoverished shrub layer would then perhaps represent the transition between oakwoods with a rich shrub layer and oakwoods with a *Rubus* layer, a transitional condition realised in sere A_0 oakwoods.

The resemblance between sere 1 and A_0 is further emphasised by a comparison of the biological spectra of all species. The data for the South Downs are obtained from the immature beechwoods of sere 1 and the three examples of Adamson's "Beechwoods on the Plateau."

	P.	Ch.	H.r.	H.s.	H.c.	G.r.	G.b.	G.rad.	T.	Total
Sere A_0	24	9	12·5	24	14	8	2·5	0	6	100
Sere 1, etc.	21·5	9·5	10·5	24	13·3	9·3	5·3	1·3	5·3	100

Thus the last of the seres on the South Downs is closely allied to the first on the Chiltern plateau.

The identity is not complete. Mercury is present in the beechwoods of A_0 and also in the open "Beechwood on the Plateau": its absence from the immature beechwood of sere 1 may be set down to incomplete migration. The early appearance of the *Rubus* layer in sere 1 is in marked contrast to its delayed appearance in A_0, where a mercury layer and not an *Oxalis* layer precedes it, and it is possible that the drier climate of the Chilterns accounts for this. But the woods are not strictly comparable: both are even-aged, but the small crowns of the beech in sere 1 contrast strongly with the heavier canopy due to the larger crowns, often supported by double leaders, of the beech in A_0, approximating to the condition of an associes (perhaps due to planting) with fuller crown development, rather than of high forest in which the trees have grown up in full competition with each other throughout their life history.

Important relationships between the seres of the South Downs and the Chilterns are diagrammatically presented on p. 503.

The modest representation of sere 1 and A_0 on their respective plateaux brings the differences between the two areas into strong relief. Deductions respecting the effects of climate must take account of this, for whereas the bulk of the soils on the plateau of the South Downs are alkaline or slightly acid with the chalk at no great distance from the surface, those of the Chiltern plateau are markedly acid. This, rather than differences in humidity, accounts for the rather meagre representation of woody species like *Acer campestre, Cornus sanguinea, Corylus avellana* (less meagre because less fastidious), *Euonymus europaeus* and *Tamus communis.* But climatic differences probably account for the absence from the Chiltern commons of *Erica cinerea,* which is locally dominant on the South Downs. On the South Downs *Polypodium vulgare* grows high up on oak stems: it has not been recorded from the Chiltern plateau and once only from the escarpment. Bryophytes, too, mantle the beech stems on the South Downs to considerable heights but are nearly

Summary of some relationships between the seres of the South Downs and the Chilterns.

Locality ...	Chiltern escarpment		South Downs escarpment	South Downs plateau			Chiltern plateau			
Height (ft.) of mature beech	67	77	80?	90	100	107 (by extrapolation)	107	82	70	60
Name of sere ...	Juniper	Hawthorn	4	3	2	1	A$_0$	A	B	C
Summarised succession of woody vegetation	Beechwood Juniper scrub	Beechwood [Ash consocies] Hawthorn scrub	Beechwood Ash consocies Chalk scrub	Beechwood Ash-oakwood Hawthorn scrub	Beechwood Ash-oakwood Hawthorn scrub	Beechwood Oakwood? Ash-oakwood Hawthorn scrub	Beechwood Oakwood Ash-oakwood Hawthorn scrub	Beechwood Oakwood Ash-oakwood Hawthorn scrub	Beechwood Oakwood Scrub?	Beechwood Oakwood
Significant layer in subsidiary vegetation of mature beechwood	Field (sanicle dominant)	Field (mercury dominant)	Field (sanicle + mercury, locally or co-dominant)	*Rubus* layer (increasing significance indicated by arrows) with a discontinuous field layer						Lower layers absent, or field layer (*Oxalis*) or *Rubus* layer local
Shrub layer in corresponding ash-oakwoods and oakwoods	—	—	—	Rich, mixed	Rich, mixed	*Corylus* prominent?	*Corylus* open layer	[*Corylus*] *Rubus*	*Rubus*	*Rubus*

confined to the bases of the trunks on the Chilterns. And the general hindrance to free colonisation of shrubs and the telescoping of the seral stages on the Chilterns is probably in part a climatic effect. This is almost certainly true for the vegetation of the escarpment, where the soils are strictly comparable with those of the escarpment of the South Downs. In this habitat *Taxus* is much more abundant and vigorous in the more humid climate of the South Downs. So too is the tolerant *Ilex*, with a range equal to that of beech. Another obvious difference is found in the response of ash, which grows freely even on the dry calcareous soils of the South Downs and much less abundantly on the Chiltern escarpment. In both areas its height growth increases on the deeper, more retentive soils of the plateau. Oak does not appear to be so responsive to climatic differences. The tolerant beech is dominant throughout, but its dimensions, both in height and girth, are greater on the South Downs than on the Chiltern escarpment. In both areas its maximum height in woods is 107 ft., already attained in A_0 and potential (calculated by extrapolation) in sere 1, but "where the unit area bears the same or a similar number of dominants the height attained is less on the Chiltern plateau than on the South Downs plateau. The different management systems alone may account for this. Height for height the beech under the selection system (Chilterns) has a larger girth, but age for age the beech in even-aged high forest (South Downs) is taller and denser" (8).

NOTE ON THE RELATION BETWEEN THE CHILTERN BEECHWOODS AND THE OAK-HORNBEAM WOODS OF HERTFORDSHIRE.

Hornbeam is sparingly present in the woods described: but in one or two beechwoods near Pulpit Hill it is common. Its occasional occurrence in the coppiced "scrubs" above Ellesborough and its common occurrence in hedgerows suggest an artificial exclusion from the high forest of oak and beech examined. In competitive equipment the hornbeam closely resembles beech but the smaller ultimate height and longevity attained prevent it from sharing dominance permanently with the latter. In an entirely natural regime hornbeam is probably a normal constituent of the pre-climax stage. Thus farther east, where the beech is only locally dominant, hornbeam is an important constituent of the copses. Whether the scarcity of the beech is due to incomplete migration, and its full occupation of the ground hindered by human interference or whether, as in the oak (*Quercus sessiliflora*)-hornbeam woods, the lowering of the water table has only recently allowed the beech to set foot in these woods, or whether some other factors were or are at work preventing its spread and dominance are matters not yet decided. But there is at present no obvious cause, except the operation of the biotic factor, to prevent beech becoming dominant.

For both the *Quercus robur*-hornbeam and *Q. sessiliflora* hornbeam woods grow on soils favourable to beech. From Salisbury's description (5) these copses do not appear to be uniform within themselves, but in some respects they bear a close, though diverging relationship to seres A_0, A and B. They also illustrate the dwindling of the shrub layer and the increasing importance of brambles and honeysuckle as well as of the acidiphilous element on the sandy loams of the sessile oak-hornbeam woods. These woods are regarded as an oak-hornbeam associes with beechwood as the potential climax.

SUMMARY OF PARTS I AND II.

The vegetation of the Chilterns reflects the direct and indirect influence of man but is essentially natural. The woods described are formed of native species whose varying behaviour is an expression of differences in soils, unaffected, except locally, by man. The description of the vegetation on the calcareous soils of the escarpment forms Part I, on the acid soils of the clay-with-flints of the plateau, Part II.

Part I. On the escarpment human interference with the vegetation is least. Two seres are recognised, distinguished floristically, vegetationally and edaphically. The juniper sere occupies the shallower and drier soils of steeper slopes and consists of grassland (not described) of shorter grasses, scrub, in which juniper is dominant, and beechwood in which *Sanicula europaea* is the most significant species of the field layer. The hawthorn sere is found on the deeper and moister soils of gentler slopes and consists of the following stages: grassland (not described) of taller grasses, a scrub with hawthorn dominant, a potential ash consocies, kept embryonic by rabbit grazing, and beechwood in which *Mercurialis perennis* is dominant in the field layer. Neither beechwood has a shrub or a *Rubus* layer.

The significant species of the juniper sere are essentially plants of drier soils: in the biological spectrum of the field layer of the sanicle beechwood the rosette hemicryptophytes and rhizome geophytes predominate. The significant species of the hawthorn sere are less xerophytic and include some characteristic of moister habitats: in the spectrum of the field layer of the mercury beechwood the scapose hemicryptophytes predominate. The vigour of species like ash and beech is greater in the hawthorn sere. From a study of the habitat and of the changes taking place during the development of the beechwoods it is concluded that hawthorn, mercury and associated herbs which characterise the hawthorn sere are excluded as significant species from the juniper sere on edaphic grounds: from the hawthorn sere, juniper and sanicle are or tend to be excluded by competition with taller growing species.

Part II. On the plateau human interference, directly by planting and indirectly through the grazing of animals, is much greater, but the vegetation of the commons provides enough material to indicate the general lines of the successional development. The three facies of the commons—grassland, bracken and heather—and the relation of shrubs and trees to each are shortly described. Independent scrub of any extent is rare and not separately dealt with.

The acid soils of the plateau show a gradient of fertility as shown by the values for acidity, exchangeable calcium and basicity and deduced from the soil texture and the kind and distribution of the organic matter both on the soil surface and in the upper soil layers. On this basis and on the basis of the floristic and vegetational variation, four seres are recognised, called respectively A_0, A, B and C. Beechwood is the final stage in all: in A_0 and A it is preceded by hawthorn scrub, developing woodland of ash and oak, and oakwood: in B and C by oakwood, developed from direct invasion of the commons by oak.

Floristically seres A_0 and A differ from B and C in the presence of many species (the ash cortège) believed to be exacting in their demands on soil minerals. In all four seres there is a common substratum of acidiphiles (e.g. *Holcus mollis*) but pronounced acidiphiles (e.g. *Deschampsia flexuosa* and *Leucobryum glaucum*) are confined to B and C. The height of ash in A_0 and A and of oak and beech in all four seres shows a steep gradient from exceptionally fine growth in A_0 to poor growth in C.

In the biological spectra the most striking feature is the changing relation between the scapose and caespitose hemicryptophytes: in A_0 the scapose forms predominate, in A the two forms are approximately equal in number, in B and C the caespitose forms outnumber the scapose and by a larger margin in C than in B.

A *Rubus* layer characterises the beechwoods: potential in the immature wood of A_0, fully developed in A and B and local in C. In the oakwoods of A_0 there is a poorly developed shrub layer of a few species, with hazel the chief; in A (except locally), B and C this is replaced by a *Rubus* layer. The *Rubus* layer seriously affects the continuity of the field layer of the relevant oakwoods and beechwoods, and in C beechwoods the field layer is absent or local only. In A_0 oakwoods where *Rubus* is not continuous a well developed field layer with a marked vernal aspect occurs.

The relationships between the scapose and caespitose hemicryptophytes in the separate seres are repeated in a milder form within seres A and B: the caespitose forms increase relatively to the scapose in the beech associes and beechwoods compared with the developing woodland and oakwood. This is an effect due to beech and is also noted from the South Down seres, suggesting a soil retrogression within the sere.

The data for acidity and the distribution of organic matter both above the soil and in the surface layers, under beech and under adjoining ash or oak, supports the conclusion that beech brings about soil degeneration. Beech therefore cannot be regarded as the climatic climax over an indefinite period. Arising out of this some suggestions are made regarding choice of trees to plant and the form of woodland management with a view to preserving soil fertility.

Floristic and vegetational comparison with the vegetation of the escarpment shows that the hawthorn sere is most closely allied to sere A_0. Particular comparison with the vegetation of the South Downs brings out the close affinity between sere 1 (including Adamson's "Beechwood on the Plateau") and sere A_0 of the Chilterns; while general comparison shows that the sanicle and mercury beechwoods of the Chilterns are equivalent to sere 4 of the South Down escarpment, that seres 3 and 2 are not represented on (or at any rate not described from) the Chilterns; and that the escarpment vegetation and seres 3, 2, 1, A_0, A, B and C form a floristic, vegetational and edaphic series in which the rate of growth of ash, oak and beech rises to a maximum in seres 1 and A_0 and falls to A for ash and to C for oak and beech. The *Rubus* layer in the beechwoods is absent from the escarpment woods but is conspicuous in all plateau beechwoods, rising to a maximum in sere 1 and falling to sere C where it is local. In the corresponding plateau seral woodlands of ash-oak and oak, the shrub layer (and derived coppice) decreases in floristic richness from sere 3 onwards, fading out in A_0 and A (local), with *Corylus avellana* the only important species, and replaced in the oakwoods of A, B and C by the *Rubus* layer. Similar changes in the shrub layer are found in oakwoods in the series Damp Oakwood—Dry Oakwood and are exemplified in the passage from the *Quercus robur—Carpinus* woods to the *Q. sessiliflora—Carpinus* woods in Hertfordshire.

The greater humidity of the South Downs induces a greater abundance and vigour of some species common to the South Downs and the Chilterns, and the droughts of spring probably aid the biotic factor in hindering the free colonisation of the Chiltern grasslands by shrubs and trees.

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ON THE VIABLE SEEDS PRESENT IN THE SOIL BENEATH PASTURES

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A knowledge of the seeds present in the soil beneath different types of vegetation is of great value in the consideration of some of the ecological problems which underlie agricultural practice and is essential in studying the effects on plant population of interspecific competition and of soil cultivation. Such knowledge is largely still an unrealised desideratum in agriculture and ecology.

A study of the seed content of pasture and arable soils has been made by Dr W. E. Brenchley (**1**), who found that a close association existed between the buried seed flora and the history of the soil. Soils underlying permanent pasture which had been continuously and closely grazed for many years were relatively deficient in seeds of any sort, but a marked difference was noticeable if the land had previously been under arable cultivation, evidence being obtained that the seeds of arable weeds may retain their viability in the soil for as long as 58 years. In soils under arable at the time of sampling, the seed flora was more varied and the seeds occurred in greater numbers. More recently Brenchley and Warington (**2, 3**) investigated the seed content of arable soils in considerable detail and again found an association between the seeds present and the treatment (in respect of manures and cultivation) which the land had received. The seeds of most species showed a marked periodicity of germination, the majority of seedlings appearing during the autumn and winter and relatively few during the late spring and summer. A definite indication was obtained that many seeds had a period of natural dormancy during which germination would not occur even under favourable conditions; a distinction was made between this phenomenon and the induced dormancy maintained in the soil by conditions unsuited to germination. In this later work no attention was given to pasture soils.

These researches have shown how interesting are the results to be obtained in this field; nevertheless little work of a critical nature has been carried out on any considerable scale by other investigators in this country. This is possibly due to the laborious nature of such experiments and to the extensive glasshouse accommodation demanded; it is, however, the more to be regretted since it is obviously undesirable to generalise from results obtained with a few fields in a single district. Natural dormancy in the seeds of many agricultural weeds has, however, been demonstrated by several workers who have carried out germination tests on seeds taken directly from the plants (**7, 10, 11**), and comprehensive studies of the soil flora of arable soils in European countries have yielded similar results to those described above (**8**, **9**, **12**).

The present study has followed closely the methods initiated by Dr Brenchley, but attention has been confined to soils lying beneath grassland, several types of the latter under widely different conditions having been examined. The primary object of the experiments has been to obtain evidence on three matters: (1) the relation between the vegetation covering the soil and the buried seed flora of the latter; (2) the importance, relative to each other within the different species, of seminal and vegetative reproduction; (3) the effects which are likely to follow in different cases on any disturbance of the existing vegetation and exposure of the soil.

METHODS.

The soils studied in the present work were too full of stones to allow of sampling with any instrument cutting out a block of definite size and shape, and a rather elaborate routine method was therefore employed. Four trenches were cut so as to isolate a column of soil about 9 in. square in cross-section (i.e. surface area) and as nearly 14 in. deep as was possible in each field. The column was then cut through at the base, removed entire, and inverted so that it rested on the surface vegetation; the first 2 in. of soil which were now uppermost (i.e. the lowest soil when *in situ*) were removed and discarded, together with parings taken from each of the four sides of the block. The soil was now removed horizontally in successive inches of depth and each separate inch placed in a paper envelope; four blocks were taken from each field. These operations were carried out with considerable care, so that the possibility of one sample contaminating another was extremely small. Subsequently, at a convenient time, the samples were crumbled by hand and a measured amount of each (about 36 cu. in.) placed in clean boxes in unheated glasshouses, the soil from this time being kept in a condition suitable for the germination of any seeds it might contain.

An analysis was made of the vegetation of each field sampled, the method employed being to estimate the tillers (i.e. single shoots) of each species which occurred, as a percentage of the total number of tillers making up the sward. (See (**6**) for details of technique.) The resulting figures show, therefore, the relationship which exists within each field between the number of shoots of the different species present, but give no indication of the amount of space covered by each nor of the number of plants, since the tillering capacity and size of the different plants are far from being the same. As, however, the tiller is the effective unit in reproduction, it forms the most satisfactory basis of analysis for the purposes of the present work.

The seedlings which developed in the soil samples were removed immediately it became possible to identify them and none in any case were allowed to produce seed. Precautions were taken against the entry of wind-carried seeds into the glasshouses, and all water given to the samples was first passed through a filter. Numerous control boxes of sterilised soil were also exposed among the samples. It is possible, therefore, to state with confidence that exceedingly few, if any, of the seedlings enumerated below have originated from external contamination.

In the case of the earliest fields sampled, the soil obtained from them has been kept for three years in a condition suitable to the germination of any contained seeds. The results obtained with these samples, however, have clearly shown that any continuance of the experiment beyond a period including two summers is unnecessary for the purposes of the present investigation, as comparatively little germination occurs afterwards. In every case the germinations recorded below occurred between the dates of sampling and the end of December, 1932.

The areas studied can be classed in accordance with their history into four groups.

A. *Natural grassland never cultivated at any time.*

(1) Llety-Ifan-hên. *Molinia* association sampled 3. xii. 1929.
(2) Ponterwyd. *Nardus* association sampled 3. iii. 1931.
(3) Ponterwyd. *Calluna* association sampled 20. iii. 1931.
(4) Waun-fawr, Frongôch. Marsh sampled 13. iii. 1930.

B. *Pasture more than* 50 *years old.*

(1) Llety-Ifan-hên. *Festuca-Agrostis* association sampled 23. vi. 1930.
(2) Capel Dewi, Peithyll, Cae brwyn[1], sampled 18. viii. 1931.
(3) Clarach, Nantllan, Cae-dan-ty, sampled 11. vi. 1931.

C. *Pasture formerly arable.*

(1) Waun-fawr, Frongôch, Barn Field, sampled 31. x. 1929.
(2) Clarach, Nantcellan, Cae Mawr, sampled 22. v. 1931.
(3) Capel Dewi, Lovesgrove, Fron Capel Dewi, sampled 14. viii. 1931.
(4) Waun-fawr, Frongôch, Brook Field, sampled 16. xii. 1929.
(5) Llanfarian, Pen-y-graig, Cae Ysgubor, sampled 1. iv. 1931.

D. *Grassland annually put up for hay, but grazed in the autumn and winter.*

(1) Wallog, Rhoscellan Fawr, Caellwyndu, sampled 6. viii. 1931.
(2) Waun-fawr, Erwgoch, Cae-tu-ôl-ty, sampled 4. viii. 1931.

In the tables relating to each field, the number of seeds which germinated at each inch are added together for all the profiles, except in the case of the totals, which are given for the individual profiles for each species.

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[1] These names are respectively those of the district, farm, and field, from which the samples were obtained.

RESULTS.

A. *Natural grassland never cultivated at any time.*

(1) *Llety-Ifan-hên. Natural* Molinia *association.*

The vegetation of this example has never, so far as is known, received cultivation of any kind and is in an entirely feral condition; the soil is peat overlying boulder clay and has a high water content over the greater part of the year. The altitude of the situation is approximately 900 ft. and the conditions and vegetation are in general typical of much "rough hill-grazing" in western Britain. The results of an analysis of the vegetation on the basis of a percentage tiller estimation was: *Molinia caerulea* 70½, *Nardus stricta* 10, *Festuca ovina* 10½, *Vaccinium Myrtillus* 3, *Calluna vulgaris* 4, *Juncus squarrosus* 2, traces of *Agrostis* spp., *Triodia decumbens*, *Erica cinerea*, *E. Tetralix*, *Potentilla erecta*, *Galium saxatile*, *Juncus communis*, *Scirpus caespitosus*, *Luzula campestris* and *Carex* spp.

Table I. *Llety-Ifan-hên. Natural* Molinia *pasture.*

Profiles *a*, *b*, *c* and *d*. Depths of profiles: *a*, 10 in.; *b*, 11 in.; *c*, 11 in.; *d*, 12 in.

	Depth in inches							Total for each profile				Aggregate total
MISCELLANEOUS PLANTS:	1	2	3	4	5	6	9	*a*	*b*	*c*	*d*	
Potentilla erecta Hampi.	12	4	1	.	.	.	.	4	12	.	1	17
Galium saxatile Linn.	2	1	2	.	.	.	.	2	1	.	2	5
Erica cinerea Linn.	281	21	.	.	.	.	.	1	22	267	12	302
Calluna vulgaris Salisb.	354	192	5	2	.	.	.	54	259	213	27	553
Rumex acetosa Linn.	4	12	.	.	.	.	.	16	.	.	.	16
Luzula campestris Br.	.	1	.	.	.	.	.	.	.	1	.	1
Juncus communis Mey.	5	3	1	.	.	.	.	5	3	1	.	9
J. articulatus Linn.	1	.	.	.	.	.	.	1	.	.	.	1
J. bulbosus Linn.	2	.	.	.	.	.	1	2	1	.	.	3
J. squarrosus Linn.	1	2	.	.	1	.	.	1	.	3	.	4
Carex spp.	24	50	16	.	.	2	.	29	33	30	.	92
Total	686	286	25	2	1	2	1					1003
GRASSES:												
Agrostis spp.	25	6	.	.	.	.	.	19	10	1	1	31
Molinia caerulea Moench.	3	.	.	.	.	.	.	1	2	.	.	3
Triodia decumbens Beauv.	2	.	.	.	.	.	.	.	2	.	.	2
Poa trivialis Linn.	1	.	.	.	.	.	.			1	.	1
Festuca ovina Linn.	2	.	.	.	.	.	.			1	.	2
Nardus stricta Linn.	4	2	.	.	.	.	.			2	.	6
Total	37	8	.	.	.	.	.					45
LEGUMES:												
Trifolium repens Linn.	2	.	.	.	.	.	.			1	.	2
Lotus corniculatus Linn.	.	1	.	.	.	.	.			.	.	1
Total	2	1	.	.	.	.	.					3

The seedlings which developed in the soil samples over a period of 3 years are shown in Table I. It is immediately apparent that there is no sort of relationship between the vegetation of the area and the seed flora of the soil beneath it; this is the more remarkable, in this case, since the herbage is grazed so lightly than an opportunity is given for all the species present in it to develop seeds. Except in the case of *Agrostis*, the number of grass seeds present is negligibly small and they are entirely confined to the first 2 in. of soil. In contrast to this, the numbers of *Carex*, *Calluna* and *Erica* seedlings are disproportionately large relative to the representation of these plants in the surface vegetation. The majority of the seedlings of *Erica cinerea* appeared in the first year, but considerable germination also occurred in the second; with *Calluna vulgaris*, germination in the second and third years was equivalent to that in the first. It is probable, therefore, that there is some natural dormancy in the seeds of these species.

The figures in the table make it clear that any disturbance of the existing vegetation will result at least temporarily in increasing the proportion of dicotyledonous plants, of *Carex*, and of *Agrostis*, relative to the dominant species; this has in fact been found to occur following the removal of turves. Should, however, such land be ploughed, any species sown in it would be entirely free of competition with native seedlings, since the deeper soil which would be brought to the surface contains no seeds.

(2) *Ponterwyd. Natural* Nardus *association.*

The soil of this area is peat, lying at an altitude of 1000 ft., no cultivation has ever occurred and the vegetation is typical of that occurring throughout Britain on the wetter portions of hill pastures. The percentage-tiller composition of the herbage was found to be as follows: *Nardus stricta* 35, *Molinia caerulea* 16, *Festuca ovina* 16½, *Agrostis* spp. 5, *Triodia decumbens* ½, *Holcus lanatus* ½, *Aira caespitosa* ½, *Vaccinium Myrtillus* 1, *Potentilla erecta* ½, *Galium saxatile* ½, *Calluna vulgaris* 15, *Erica cinerea* 3½, *E. Tetralix* 3½, *Scirpus caespitosus* 1½, *Juncus squarrosus* ½, traces of *J. communis*, *J. bufonius* and *Carex* spp.

Table II. *Ponterwyd. Natural* Nardus *pasture.*

Profiles *a*, *b*, *c* and *d*. Depths of profiles: *a*, 12 in.; *b*, 11 in.; *c*, 12 in.; *d*, 10 in.

	Depths in inches									Total for each profile				Aggregate total
MISCELLANEOUS PLANTS:	1	2	3	4	5	6	7	8	9	*a*	*b*	*c*	*d*	
Ranunculus repens Linn.	1	.	.	.	.	.	.	.	.	1	.	.	.	1
Potentilla erecta Hampi.	18	13	4	.	.	.	.	.	.	20	2	2	11	35
Galium saxatile Linn.	39	17	5	1	.	.	.	.	.	44	10	2	6	62
Vaccinium Myrtillus Linn.	1	1	.	.	.	.	.	.	.	1	.	1	.	2
Erica cinerea Linn.	58	41	1	2	.	.	.	.	.	2	67	1	32	102
Calluna vulgaris Salisb.	257	61	6	.	6	1	.	.	.	43	279	4	5	331
Juncus communis Mey.	6	14	31	18	16	5	3	3	1	25	.	4	68	97
J. squarrosus Linn.	3	12	15	4	4	1	.	.	.	8	5	17	9	39
J. bufonius Linn.	2	11	15	21	15	6	.	.	.	23	.	2	45	70
J. bulbosus Linn.	3	12	56	28	17	15	10	3	2	1	.	10	135	146
Carex spp.	121	134	143	59	19	9	1	.	.	183	41	73	189	486
Total	509	316	276	133	77	37	14	6	3					1371
GRASSES:														
Agrostis spp.	18	8	1	.	.	.	.	.	.	4	1	4	18	27
Triodia decumbens Beauv.	5	4	.	.	.	.	.	.	.	5	.	4	.	9
Festuca ovina Linn.	3	.	.	.	.	.	.	.	.	3	.	.	.	3
Nardus stricta Linn.	1	.	.	.	.	.	.	.	.	.	1	.	.	1
Total	27	12	1	.	.	.	.	.	.					40

It will be seen from Table II that the seedling population growing out of this soil is greater than in the case of the *Molinia* pasture, although the experiment has extended over a much shorter time, and that a large number of species has contributed materially to it. The extreme scarcity of grass seedlings other than those of *Agrostis* is, however, again shown, as also is the predominance of seedlings of *Calluna*, *Erica* and *Carex*. Evidence of dormancy in the seeds was again obtained for *Calluna vulgaris* and *Erica cinerea* and also for *Galium saxatile* and *Carex*. The most striking feature of Table II is the occurrence of large numbers of rushes none of the species of which is present to any considerable extent in the vegetation of the soil, and it is noteworthy that the greatest density of seedlings is from the third, fourth and fifth inches. This is in marked contrast to the distribution of all the other species of plants, and would apparently suggest that rushes were formerly more prevalent in this area; it is difficult to see, however, how this can have taken place under such uniform conditions as have obtained indefinitely (so far as is known) at this place. With all four species of *Juncus* there is very definite evidence of natural dormancy in the seeds.

The complete absence of *Scirpus caespitosus*, both here and in the case of the *Molinia* pasture, is remarkable, since this plant occurs in some quantity on both areas and flowers profusely.

It is extremely probable that any disturbance of this land would result in a great increase in the number of rushes, which might easily, in fact, become the dominant members of the vegetation.

(3) *Ponterwyd. Natural* Calluna *association.*

The altitude of this area is 1100 ft.; the soil is peat overlying gravel. The result of an analysis of the vegetation was: *Molinia caerulea* 10, *Nardus stricta* 20, *Festuca ovina* 10, *Agrostis* spp. 1½, *Vaccinium Myrtillus* 2, *Calluna vulgaris* 46½, *Erica cinerea* 1½, *E. Tetralix* 1½, *Juncus squarrosus* 3, *Carex* spp. 4, traces of *Juncus communis* and *J. articulatus*.

Table III. *Ponterwyd. Natural* Calluna *association.*

Profiles *a*, *b*, *c* and *d*. Depths of profiles: *a*, 12 in.; *b*, 9 in.; *c*, 5 in.; *d*, 11 in.

	Depths in inches						Total for each profile				Aggregate total
	1	2	3	4	5	6	*a*	*b*	*c*	*d*	
MISCELLANEOUS PLANTS:											
Ranunculus repens Linn.	.	1	.	.	.	.	.	.	.	1	1
Galium saxatile Linn.	7	2	.	.	.	.	9	.	.	.	9
Erica cinerea Linn.	123	41	.	.	.	.	52	31	2	79	164
Calluna vulgaris Salisb.	544	62	.	.	.	.	132	288	76	110	606
Juncus communis Mey.	3	2	2	.	1	.	.	5	2	1	8
J. articulatus Linn.	1	.	.	.	.	.	.	.	1	.	1
J. bufonius Linn.	.	.	.	.	1	.	.	1	.	.	1
J. bulbosus Linn.	1	.	1	1	1	2	.	5	1	.	6
J. squarrosus Linn.	1	2	.	.	.	.	1	.	1	1	3
Carex spp.	47	60	6	.	.	.	38	25	9	41	113
Total	727	170	9	1	3	2					912
GRASSES:											
Agrostis spp.	2	.	.	1	.	1	.	1	1	2	4

As would be expected, the seed flora of this area (Table III) is extremely limited both in species and number. Delayed germination indicative of natural dormancy in the seeds has again been found to occur in the cases of *Calluna, Erica* and *Carex.*

The relatively small number of seeds present in the lower soil of this area, and of the *Molinia* and *Festuca-Agrostis* areas described elsewhere in this paper, and the possibility that this may be due to the absence of earthworms, have been discussed in a previous publication (**4**).

(4) *Waun-fawr, Frongôch. Marsh.*

The vegetation of this example was analysed as follows: *Molinia caerulea* ½, *Holcus lanatus* 52, *Agrostis* spp. 25, *Festuca rubra* 7, *Cynosurus cristatus* ½, *Poa trivialis* 1½, *Anthoxanthum odoratum* 1, *Glyceria fluitans*—a trace, *Luzula campestris* 1½, *Carex* spp. ½, *Juncus* spp. 9, *Lotus corniculatus* ½, and *Hypochoeris radicata, Prunella vulgaris, Rumex acetosa, Carduus palustris* and *Ranunculus* spp., together making up 1: traces were also present of *Triodia decumbens, Trifolium repens* and *T. pratense.* Much of the ground also is covered with *Sphagnum.* The soil is peat overlying clay, but contains a good deal of calcium since it receives drainage from cultivated fields; the altitude is about 300 ft.

It will be seen from Table IV that the seed flora is exceedingly varied but shows a general relationship to that of the surface vegetation. The numbers of seedlings of *Juncus, Lotus, Agrostis* and *Carex,* are, however, disproportionately large. *Anagallis tenella, Juncus triglumis* and *J. bulbosus* are peculiar in occurring in greater numbers at some depth than in the surface layer.

With the possible exception of *Sonchus oleraceus,* no species typical of arable land occur, although fields under arable cultivation adjoin this area.

Delayed germination occurred in the seeds of *Juncus communis, J. bufonius, J. triglumis, Carex, Epilobium montanum, Anagallis tenella* and *Poa trivialis*; in the case of *Juncus bulbosus* and *J. articulatus* no germination at all took place during the first year.

This area is typical of much land throughout Britain that is possibly improvable by cultivation; it is significant, therefore, that the present results indicate that any exposure of bare ground in such cultivation is inadvisable, since this would almost certainly result in increased numbers of rushes and hence in a sward of even lower value.

B. *Pasture more than 50 years old.*

(1) *Llety-Ifan-hên. Natural* Festuca-Agrostis *association.*

This area is about 900 ft. above sea-level; the soil is peat overlying gravel which comes within 4 or 5 in. of the surface. The vegetation is typical of many hill pastures occurring on slopes with good drainage; the analysis was: *Festuca ovina* 55½, *Agrostis* spp. 29, *Molinia caerulea* 4½, *Potentilla erecta* 4, *Calluna vulgaris* 4½, *Erica cinerea* 2½, traces of *Triodia decumbens, Luzula campestris, Vaccinium Myrtillus, Galium saxatile, Erica Tetralix, Juncus squarrosus* and *Carex* spp. There is evidence that at some former time this land has been ploughed, possibly during the Napoleonic wars: the herbage has, however, returned to a feral condition.

Table IV. *Frongôch marsh.*

Profiles *a*, *b*, *c* and *d*. Depth of all profiles 12 in.

	Depths in inches												Total for each profile				Aggregate total
	1	2	3	4	5	6	7	8	9	10	11	12	*a*	*b*	*c*	*d*	
MISCELLANEOUS PLANTS:																	
Ranunculus repens Linn.	3	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	3
R. Flammula Linn.	60	14	9	5	.	1	.	.	.	.	.	.	1	52	36	.	89
Cardamine hirsuta Linn.	9	2	.	.	.	.	.	.	.	.	.	.	.	2	9	.	11
Viola canina Linn.	.	2	1	.	.	.	.	.	.	.	.	.	2	.	1	.	3
Sagina procumbens Linn.	33	.	.	.	.	.	.	.	.	.	.	.	.	32	1	.	33
Cerastium vulgatum Linn.	21	.	.	.	.	.	.	.	.	.	.	.	.	.	21	.	21
Stellaria media Cyrill.	3	3	.	.	.	.	.	.	.	.	.	.	1	3	2	.	6
S. uliginosa Murr.	43	.	.	.	.	.	.	.	.	.	.	.	1	.	42	.	43
Potentilla erecta Hampi.	6	3	1	.	.	.	.	.	.	.	.	.	2	1	.	7	10
P. reptans Linn.	3	2	1	.	.	.	.	.	.	.	.	.	.	6	.	.	6
Epilobium palustre Linn.	4	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	4
E. montanum Linn.	15	17	.	.	.	1	.	.	.	.	.	.	5	13	15	.	33
Hydrocotyle vulgaris Linn.	.	3	.	.	.	.	.	.	.	.	.	.	.	3	.	.	3
Galium saxatile Linn.	15	17	.	.	.	.	.	.	.	.	.	.	.	29	3	.	32
Scabiosa Succisa Linn.	6	.	.	.	.	.	.	.	.	.	.	.	.	1	5	.	6
Sonchus oleraceus Linn.	.	6	1	.	.	.	.	.	.	.	.	.	7	.	.	.	7
Senecio Jacobaea Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Chrysanthemum Leucanthemum Linn.	4	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	4
Carduus palustris Linn.	9	2	.	.	.	.	.	.	.	.	.	.	2	3	6	.	11
Achillea Ptarmica Linn.	1	1	3	.	.	.	.	.	.	.	.	.	.	.	.	5	5
Campanula hederacea Linn.	23	12	7	2	.	.	.	.	.	.	.	.	.	1	.	43	44
Anagallis tenella Linn.	17	15	23	19	14	7	4	.	.	.	.	.	1	46	.	52	99
Myosotis scorpioides Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Digitalis purpurea Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Veronica serpyllifolia Linn.	2	14	.	.	.	.	.	.	.	.	.	.	1	15	.	.	16
Mentha aquatica Linn.	6	1	.	.	.	.	.	.	.	.	.	.	1	.	6	.	7
Scutellaria minor Linn.	8	8	.	.	.	.	.	.	.	.	.	.	8	8	.	.	16
Rumex acetosa Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Orchis maculata Linn.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1
Luzula campestris Br.	29	16	7	3	.	.	.	.	.	.	.	.	28	17	.	10	55
Juncus communis Mey.	256	100	70	53	27	22	10	4	1	.	.	.	246	136	128	33	543
J. articulatus Linn.	69	34	41	20	5	10	4	.	.	.	.	.	46	81	56	.	183
J. bufonius Linn.	94	122	32	18	17	3	6	7	.	.	1	.	19	255	9	17	300
J. triglumis Linn.	3	2	2	6	3	11	6	11	17	.	.	.	.	18	43	.	61
J. bulbosus Linn.	2	5	13	22	18	18	15	10	33	4	1	.	32	46	58	5	141
J. squarrosus Linn.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	1
Scirpus setaceus Linn.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Carex spp.	152	79	104	87	89	64	25	5	2	.	.	1	217	181	48	162	608
Total	901	480	316	236	173	137	70	37	53	4	2	1					2410
GRASSES:																	
Anthoxanthum odoratum	6	.	.	.	.	.	.	.	.	.	.	.	.	4	1	1	6
Agrostis spp.	133	36	12	3	1	.	.	.	2	.	2	.	58	61	10	60	189
Holcus lanatus Linn.	24	1	.	.	.	.	.	.	.	.	.	.	3	5	16	1	25
Triodia decumbens Beauv.	.	1	.	1	.	.	.	.	.	.	.	.	1	.	.	1	2
Molinia caerulea Moench.	.	6	3	.	.	.	.	.	.	.	.	.	.	8	1	.	9
Poa trivialis Linn.	28	4	1	.	2	.	.	1	.	.	1	.	2	3	27	5	37
Glyceria fluitans Sm.	4	1	.	.	.	2	.	.	.	.	1	.	1	1	4	2	8
Festuca rubra Linn.	11	.	1	2	1	.	.	.	.	.	.	.	1	9	2	3	15
Nardus stricta Linn.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	1
Total	206	49	17	7	4	2	.	1	2	.	4	.					292
LEGUMES:																	
Trifolium pratense Linn.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	1
T. repens Linn.	4	8	5	.	.	.	.	1	.	.	.	.	.	7	11	.	18
Lotus corniculatus Linn.	113	46	31	1	.	.	.	.	.	.	.	.	125	58	.	8	191
Total	117	54	36	1	.	.	1	1	.	.	.	.					210

Table V shows how limited in number and species is the seed flora of the soil. No arable weeds indicative of the former cultivation occur.

Delayed germination was again shown in the case of *Calluna vulgaris* and *Galium saxatile.*

Table V. *Llety-Ifan-hên. Natural* Festuca-Agrostis *pasture.*

Profiles *a*, *b*, *c* and *d*. Depths of profiles: *a*, 12 in.; *b*, 10 in.; *c* and *d*, 12 in.

	Depths in inches						Total for each profile				Aggregate total
MISCELLANEOUS PLANTS:	1	2	3	4	5	6	*a*	*b*	*c*	*d*	
Potentilla erecta Hampi.	9	16	1	1	.	.	1	16	2	8	27
Galium saxatile Linn.	17	14	5	1	1	.	6	21	5	6	38
Erica cinerea Linn.	1	.	.	.	.	.	.	1	.	.	1
Calluna vulgaris Salisb.	48	99	25	7	4	4	10	129	14	34	187
Veronica officinalis Linn.	2	.	.	.	.	.	2	.	.	.	2
Carex spp.	8	17	5	.	.	.	.	19	7	4	30
Total	85	146	36	9	5	4					285
GRASSES:											
Agrostis spp.	53	39	1	1	2	1	10	44	3	40	97
Triodia decumbens Beauv.	.	1	.	1	.	.	.	1	.	1	2
Poa trivialis Linn.	1	.	.	1	.	.	.	.	.	2	2
Festuca ovina Linn.	.	4	1	.	.	.	.	5	.	.	5
Total	54	44	2	3	2	1					106

(2) *Capel Dewi, Peithyll, Cae brwyn.*

This and the ensuing examples are all representative of cultivated grassland at low altitudes. The present field has not been ploughed within memory, and has been kept closely grazed as pasture. The sward was analysed as follows: *Lolium perenne* 23, *Cynosurus cristatus* 17, *Poa trivialis* 16, *P. annua* ½, *Festuca rubra* 13, *Holcus lanatus* 14½, *Agrostis* spp. 10½, *Anthoxanthum odoratum* ½, *Dactylis glomerata* ½, *Trifolium repens* 2½, *T. pratense* ½, traces of *T. minus*, *Juncus communis* and *Carex* spp. and *Plantago lanceolata*, *Bellis perennis*, *Prunella vulgaris*, *Luzula campestris* and *Achillea Millefolium* together making 1½.

The seedlings growing out of this soil are given in Table VI. It will be seen that, although many species occur, the total number of seedlings is small. Some of the species are typical arable weeds (e.g. *Chenopodium album*, *Polygonum convolvulus* and *Euphorbia Helioscopia*), but their distribution in the soil is not such as to suggest that they are survivors from some period of arable cultivation, but rather that they have been introduced by cattle. There are also species characteristic of inferior, badly drained pasture, and the seeds of these are present in considerable numbers; it is noticeable that they are best represented some distance below the surface, and it is possible that these are relics of a time when the land was less intensively grazed than is the case now.

The proportion of grass seedlings is high compared with that shown by the other tables, but is much lower than might have been expected from the composition of the sward; the lack of *Lolium perenne* and *Cynosurus cristatus* seedlings is remarkable.

(3) *Clarach, Nantllan, Cae-dan-ty.*

This field has been kept as pasture for 60 years. The result of an analysis of the sward was: *Lolium perenne* 27½, *Dactylis glomerata* 7, *Cynosurus cristatus* 6½, *Poa trivialis* 22, *P. annua* 1½, *Festuca rubra* 9, *Holcus lanatus* 7, *Agrostis* spp. 13, *Trifolium repens* 5½, traces of *Juncus communis*, *Luzula campestris*, *Trifolium minus*, *T. pratense* and *Carex* spp., and *Cerastium vulgatum*, *Bellis perennis*, *Plantago lanceolata* and *Ranunculus* spp. together making 1.

Table VI. *Peithyll.*

Profiles *a*, *b*, *c* and *d*. Depth of all profiles 12 in.

	Depths in inches												Total for each profile				Aggregate total
MISCELLANEOUS PLANTS:	1	2	3	4	5	6	7	8	9	10	11	12	*a*	*b*	*c*	*d*	
Ranunculus repens Linn.	3	10	2	3	1	.	.	.	.	1	.	.	3	4	12	1	20
Brassica Sinapis Visiani	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Sagina procumbens Linn.	30	2	1	2	.	.	.	2	.	.	.	.	35	.	2	.	37
Cerastium vulgatum Linn.	33	9	7	1	.	.	.	.	2	.	.	1	2	12	28	11	53
Stellaria media Cyrill.	1	1	1	.	.	.	.	.	1	.	.	.	1	1	.	2	4
S. uliginosa Murr.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	1
Hypericum humifusum Linn.	.	.	1	2	1	1	.	.	.	.	1	1	2	2	1	2	7
Potentilla reptans Linn.	.	1	1	2	1	1	.	.	1	.	.	.	3	1	1	2	7
Alchemilla arvensis Scop.	.	.	2	1	.	.	.	.	.	.	.	.	.	3	.	.	3
Epilobium montanum Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Taraxacum officinale Web.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	4
Bellis perennis Linn.	26	12	.	.	1	1	.	.	.	.	.	.	.	1	8	31	40
Leontodon hispidus Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Carduus arvensis Robs.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Achillea Millefolium Linn.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2
Anagallis arvensis Linn.	.	.	.	1	.	1	.	.	.	.	.	.	2	.	.	.	2
A. tenella Linn.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	1
Veronica serpyllifolia Linn.	4	5	5	4	.	2	.	.	.	.	.	.	10	8	.	2	20
Prunella vulgaris Linn.	20	26	5	2	2	3	.	.	1	.	.	.	3	9	28	19	59
Plantago lanceolata Linn.	1	2	.	1	.	.	.	.	.	.	.	.	.	1	2	1	4
Chenopodium album Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Polygonum convolvulus Linn.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	1
Rumex acetosa Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Euphorbia Helioscopia Linn.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	1
Luzula campestris Br.	2	.	2	1	.	.	.	.	.	.	.	.	.	.	4	1	5
Juncus communis Mey.	6	3	5	12	4	7	2	2	.	.	.	1	20	8	3	11	42
J. articulatus Linn.	.	.	.	1	.	.	1	.	.	.	.	.	1	.	.	1	2
J. bufonius Linn.	1	4	1	4	1	.	.	1	.	.	.	.	10	.	.	2	12
Carex spp.	9	12	5	1	6	3	3	1	1	2	1	.	8	11	10	15	44
Total	145	90	38	38	18	20	6	6	7	3	2	4					377
GRASSES:																	
Anthoxanthum odoratum Linn.	1	2	.	.	.	.	.	.	.	.	.	.	.	2	1	.	3
Agrostis spp.	48	34	22	23	15	8	1	3	1	1	.	.	41	33	21	61	156
Holcus lanatus Linn.	7	5	1	.	.	.	.	.	.	.	.	.	1	2	10	.	13
Dactylis glomerata Linn.	.	1	.	.	.	.	1	.	.	.	.	.	2	.	.	.	2
Poa trivialis Linn.	25	20	11	7	.	4	4	.	.	.	.	.	18	21	27	5	71
P. annua Linn.	10	3	4	2	3	4	1	.	.	2	1	.	21	.	2	7	30
Festuca rubra Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Lolium perenne Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Nardus stricta Linn.	.	7	4	.	.	.	.	.	.	.	.	.	.	5	6	.	11
Total	92	73	42	32	18	16	7	3	1	3	1	.					288
LEGUMES:																	
Trifolium pratense Linn.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1
T. repens Linn.	2	5	9	2	.	3	1	.	.	.	.	.	3	10	7	2	22
Total	2	6	9	2	.	3	1	.	.	.	.	.					23

Among the species arising from the soil of this field (Table VII) are a number characteristic of arable soil, viz. *Fumaria officinalis*, *Anagallis arvensis* and *Chenopodium album*. The distribution of these in the soil is suggestive of their having been buried some time, but it is doubtful in the extreme whether they can be regarded as survivors from the time of arable cultivation. The seeds of such plants can be introduced into the soil beneath pasture in two ways: from arable plants growing on small patches of bare soil such as are present in almost all grassland, and from the dung of animals. In the latter connection, the annual dressings of dung which it is customary to apply each winter to pastures must introduce large quantities of seed into the soil.

Table VII. *Clarach.*

Profiles *a*, *b*, *c* and *d*. Depths of profiles: *a*, *b*, *c*, 12 in.; *d*, 10 in.

	Depths in inches												Total for each profile				Aggregate total
MISCELLANEOUS PLANTS:	1	2	3	4	5	6	7	8	9	10	11	12	*a*	*b*	*c*	*d*	
Ranunculus repens Linn.	3	29	21	14	3	3	3	6	2	.	6	1	2	19	43	27	91
Fumaria officinalis Linn.	.	.	.	4	.	6	3	.	.	.	.	.	.	4	6	3	13
Brassica Sinapis Visiani	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	1
Senebiera Coronopus Poir.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1
Sagina procumbens Linn.	59	15	11	28	8	3	1	3	4		.	1	37	63	19	14	133
Cerastium vulgatum Linn.	37	34	7	2	1	2	2	1	.	.	.	1	21	6	9	51	87
Stellaria media Cyrill.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	1
Elatine Hydropiper Linn.	2	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	2
Hypericum humifusum Linn.	.	.	.	.	.		1	.	.	.	.	.	.	.	1	.	1
Alchemilla arvensis Scop.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	1
Taraxacum officinale Web.	.	16	.	.	.	.	.	.	.	.	.	1	2	.	9	6	17
Bellis perennis Linn.	7	2	1	.	1	.	2	.	1	.	1	.	5	.	7	3	15
Senecio vulgaris Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Anagallis arvensis Linn.	.	5	7	5	10	7	7	8	4	2	2	1	19	19	6	14	58
Veronica serpyllifolia Linn.	3	10	4	6	4	1	4	.	2	2	1	1	10	12	6	10	38
Galeopsis Tetrahit Linn.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Plantago lanceolata Linn.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	1
P. major Linn.	3	20	26	10	7	9	3	.	1	.	1	.	23	.	57	.	80
Chenopodium album Linn.	.	1	.	.	2	2	.	1	.	.	.	.	4	1	.	1	6
Polygonum aviculare Linn.	2	.	1	.	1	.	.	.	1	.	.	.	2	1	2	.	5
P. Persicaria Linn.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Rumex acetosa Linn.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Euphorbia Helioscopia Linn.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Urtica dioica Linn.	5	4	4	1	1	.	1	1	2	2	.	1	14	3	2	3	22
Luzula campestris Br.	.	1	1	.	.	.	.	.	1	.	.	.	.	3	.	.	3
Juncus communis Mey.	108	67	81	20	18	25	7	10	2	2	2	2	30	231	37	46	344
J. articulatus Linn.	1	4	3	.	.	.	.	.	1	.	.	.	2	3	3	1	9
J. bufonius Linn.	.	6	5	1	2	1	.	1	3	.	.	1	3	10	4	3	20
Carex spp.	1	12	.	1	.	1	.	.	.	1	.	.	5	5	4	2	16
Scirpus setaceus Linn.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Total	232	227	177	92	58	60	36	32	24	10	13	10					971
GRASSES:																	
Agrostis spp.	43	55	29	12	5	1	6	2	1	1	.	1	30	55	49	22	156
Holcus lanatus Linn.	3	11	5	3	1	1	.	1	.	.	.	.	.	2	5	18	25
Cynosurus cristatus Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Dactylis glomerata Linn.	3	4	4	1	.	.	1	.	.	.	.	.	6	5	2	.	13
Poa trivialis Linn.	39	35	24	19	8	4	4	4	4	4	3	.	43	33	47	25	148
P. annua Linn.	125	160	104	40	31	25	19	23	9	23	9	17	180	88	282	35	585
Total	214	265	166	75	45	31	30	30	14	28	12	18					928
LEGUMES:																	
Trifolium pratense Linn.	.	.	1	.	1	.	1	.	.	.	.	.	.	.	3	.	3
T. repens Linn.	5	14	19	7	6	6	.	2	1	1	.	.	20	18	14	9	61
T. minus Sm.	1	1	7	1	.	1	.	.	1	.	.	.	2	4	1	5	12
Total	6	15	27	8	7	7	1	2	2	1	.						76

The number of *Poa annua* seedlings is disproportionately large, but, as in the previous example, *Lolium perenne* and *Cynosurus cristatus* are scarcely represented, although abundant in the surface vegetation. The large number of seedlings of *Juncus communis* is not anomalous since this plant is abundant in the immediate vicinity of the field. The occurrence of the rare *Elatine Hydropiper* is noteworthy.

Delayed germination was shown by *Sagina procumbens* and the three species of *Juncus*.

C. *Grassland formerly arable.*

(1) *Waun-fawr, Frongôch, Barn Field.*

In this case the land has been under grass for 50 years, but the quality of the herbage is poor, being made up in considerable part of weeds such as *Ranunculus repens* and *Juncus bufonius*. The result of an analysis was: *Lolium perenne* 17, *Dactylis glomerata* ½, *Cynosurus cristatus* 22, *Poa trivialis* 19, *Festuca rubra* 1, *Holcus lanatus* 11, *Agrostis* spp. 15, *Anthoxanthum odoratum* 1½, *Juncus* spp. 7, *Trifolium repens* 4, traces of *Poa annua*, *Trifolium minus* and *Carex* spp., and *Bellis perennis*, *Prunella vulgaris*, *Taraxacum officinale*, and *Ranunculus* spp. together making 2.

The seedlings obtained are given in Table VIII, the number of dicotyledons being very great. The density in the soil of seeds of *Ranunculus repens* is remarkable. Some of the weeds are typically arable (e.g. *Chenopodium album*, *Polygonum Persicaria* and *Gnaphalium uliginosum*) but they are few both in species and number. The proportion of grass seedlings in this example is very small relative to that of dicotyledonous plants, and in comparison with the preceding field all the species of the former, except *Holcus lanatus*, show a considerable diminution. This is probably to be explained by the fact that the field has been closely grazed for many years, having been employed as a paddock.

Delayed germination occurred in the seeds of *Ranunculus repens*, *Bellis perennis*, *Sagina procumbens*, *Gnaphalium uliginosum*, *Juncus communis*, *J. bufonius*, *J. articulatus*, *Scirpus setaceus*, *Trifolium repens*, *T. minus* and *Poa trivialis*.

(2) *Clarach, Nantcellan, Cae Mawr.*

This pasture has been in existence for 40 years, and the turf is in exceptionally good condition; the percentage tiller composition was as follows: *Lolium perenne* 20, *Cynosurus cristatus* 6, *Alopecurus pratense* 2, *Poa trivialis* 41, *P. annua* 5, *Festuca rubra* 4, *Holcus lanatus* 5, *Agrostis* spp. 9, *Festuca elatior* 4½, *Trifolium repens* 2, and *Cerastium vulgatum*, *Bellis perennis*, *Plantago lanceolata*, *Achillea Millefolium*, *Sagina procumbens*, *Rumex acetosa*, *Taraxacum officinale*, *Prunella vulgaris* and *Ranunculus* spp. together making 1½.

Table IX shows the seedlings obtained, and it is apparent that a considerable number are of species typical of arable land. Since in every such case the seeds occur some distance beneath the surface it is possible that these are relics of the arable cultivation which the field received 40 years before the time of sampling. The distribution of charlock seeds is noteworthy in this respect, since it is generally believed by farmers that these seeds can remain dormant in the soil for long periods: it is clear that what would apparently be evidence of this would be obtained were the present field to be ploughed.

The number of seedlings of *Poa trivialis*, *P. annua*, *Trifolium repens* and *Agrostis* spp. is extremely small considering their representation in the sward;

this is possibly due to the field having been intensively grazed on the rotational system for 4 years previous to the time of sampling.

Table VIII. *Barn Field.*

Profiles *a*, *b*, *c* and *d*. Depth of all profiles 12 in.

	Depths in inches												Total for each profile				Aggregate total
	1	2	3	4	5	6	7	8	9	10	11	12	*a*	*b*	*c*	*d*	
MISCELLANEOUS PLANTS:																	
Ranunculus repens Linn.	82	264	427	474	194	109	55	28	11	18	24	9	431	347	778	139	1695
R. Flammula Linn.	1	.	.	1	.	.	1	.	.	.	.	.	.	1	2	.	3
Capsella Bursa-pastoris Moench.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	1
Spergula arvensis Linn.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	1
Sagina procumbens Linn.	46	13	11	8	4	3	1	1	.	.	.	.	20	4	55	8	87
Cerastium vulgatum Linn.	14	19	4	6	4	3	1	.	1	1	.	1	16	4	5	29	54
Hypericum humifusum Linn.	.	.	.	1	.	2	.	.	.	.	.	.	.	2	.	1	3
Potentilla erecta Hampi.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	1
P. reptans Linn.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	1
Rubus fruticosus Linn.	.	.	.	.	.		.	1	.	.	.	.	.	.	.	1	1
Heracleum Sphondylium Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Anthemis Cotula Linn.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	1
Taraxacum officinale Web.	17	2	4	2	.	2	1	1	1	1	.	1	3	3	12	14	32
Gnaphalium uliginosum Linn.	1	5	4	10	20	25	17	6	12	2	2	.	10	61	25	8	104
Sonchus oleraceus Linn.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	1
Bellis perennis Linn.	133	133	20	9	.	11	10	10	.	.	1	.	225	17	45	40	327
Chrysanthemum Leucanthemum Linn.	.	2	3	1	.	.	.	.	.	.	.	.	2	2	.	2	6
Senecio vulgaris Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Anagallis arvensis Linn.	3	1	2	.	2	.	2	3	2	.	.	.	.	2	1	12	15
Centunculus minimus Linn.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	1
Prunella vulgaris Linn.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2
Mentha aquatica Linn.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	2	2
Plantago lanceolata Linn.	5	10	8	1	.	.	.	.	.	.	.	1	2	3	7	13	25
P. major Linn.	2	2	3	1	4	5	5	3	4	.	.	.	7	4	3	15	29
Digitalis purpurea Linn.	.	1	.	2	.	.	.	1	.	.	.	.	3	.	1	.	4
Veronica serpyllifolia Linn.	6	1	4	4	1	4	5	3	1	.	1	.	5	6	7	12	30
Chenopodium album Linn.	.	.	1	.	2	3	.	.	.	.	.	.	.	1	4	1	6
Polygonum aviculare Linn.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	1
P. Persicaria Linn	.	.	.	1	5	1	.	.	1	.	.	.	.	2	4	2	8
Rumex obtusifolius Linn.	2	6	81	23	3	1	.	1	.	.	.	.	.	116	.	1	117
R. acetosa Linn.	2	2	.	1	.	.	.	.	.	.	.	2	1	1	3	2	7
R. acetosella Linn.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	1
Luzula campestris Br.	1	1	.	.	.	.	.	.	.	.	.	.	.	1	1	.	2
Juncus communis Mey.	4	16	12	10	6	18	10	3	2	.	.	4	2	33	29	21	85
J. articulatus Linn.	3	.	3	3	.	2	3	2	.	.	.	.	1	1	8	6	16
J. bufonius Linn.	67	118	74	62	83	113	102	35	27	16	6	8	198	198	197	118	711
J. triglumis Linn.	.	.	.	.	.	.	1	1	.	1	.	.	1	.	2	.	3
J. bulbosus Linn.	.	.	1	.	.	.	.	1	1	1	2	.	2	1	1	2	6
Scirpus setaceus Linn.	1	3	.	3	7	9	6	3	.	1	2	.	10	11	8	6	35
Carex spp.	.	1	3	6	5	5	3	.	1	.	.	.	6	6	8	4	24
Total	393	601	665	631	342	316	227	104	66	41	38	20					3450
GRASSES:																	
Anthoxanthum odoratum Linn.	.	3	3	.	1	.	.	.	.	.	.	.	6	1	.	.	7
Alopecurus pratensis Linn.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	3	.	3
Agrostis spp.	16	19	8	6	4	3	3	2	.	.	.	.	7	10	39	5	61
Holcus lanatus Linn.	2	12	18	1	2	.	.	.	.	.	.	1	10	10	10	6	36
Cynosurus cristatus Linn.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	1
Dactylis glomerata Linn.	.	.	.	.	1	.	.	.	.	.	.	2	1	2	.	.	3
Poa trivialis Linn.	25	35	12	13	5	9	2	2	.	.	4	2	30	38	30	11	109
P. annua Linn.	3	.	3	.	1	1	.	.	.	.	.	.	2	.	1	5	8
Festuca rubra Linn.	1	1	.	1	.	1	1	1	.	1	.	.	6	.	1	.	7
Total	47	70	44	24	15	14	6	5	.	1	4	5					235
LEGUMES:																	
Trifolium pratense Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
T. repens Linn.	11	15	5	6	1	.	.	4	.	.	.	1	13	3	9	18	43
T. minus Sm.	.	9	1	1	.	2	.	.	.	.	.	.	4	1	4	4	13
Lotus corniculatus Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Total	11	26	6	7	1	2	.	4	.	.	.	1					58

Table IX. *Nantcellan.*

Profiles *a*, *b*, *c* and *d*. Depth of all profiles 12 in.

	Depths in inches												Total for each profile				Aggregate total
MISCELLANEOUS PLANTS:	1	2	3	4	5	6	7	8	9	10	11	12	*a*	*b*	*c*	*d*	
Ranunculus repens Linn.	10	102	43	21	19	21	15	7	2	3	2	.	38	112	48	47	245
Fumaria officinalis Linn.	.	.	1	5	1	2	.	.	.	.	.	.	1	3	5	.	9
Brassica Sinapis Visiani	.	1	2	7	9	13	6	.	4	3	2	.	2	23	.	22	47
B. campestris Linn.	.	1	.	.	.	.	.	3	1	2	.	.	.	3	.	4	7
Viola arvensis Murr.	.	.	.	.	1	.	.	.	.	.	.	1	1	.	.	1	2
Sagina procumbens Linn.	241	235	87	57	20	6	1	2	.	.	.	.	65	37	488	59	649
Cerastium vulgatum Linn.	9	9	3	3	.	4	.	1	.	.	.	.	5	13	6	5	29
Hypericum humifusum Linn.	1	2	4	3	2	.	.	1	2	1	.	1	3	1	4	9	17
Alchemilla arvensis Scop.	.	.	.	1	1	.	5	1	.	.	.	.	6	1	.	1	8
Sonchus oleraceus Linn.	.	2	1	.	.	.	.	.	.	.	.	.	.	1	1	1	3
Bellis perennis Linn.	7	9	2	1	.	.	1	.	.	.	.	.	3	4	10	3	20
Leontodon hispidus Linn.	1	2	2	.	.	.	.	.	.	.	.	.	.	.	5	.	5
Carduus arvensis Robs.	.	4	.	.	.	.	.	.	.	.	.	.	1	3	.	.	4
C. lanceolatus Linn.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	1	1	2
Lapsana communis Linn.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Anagallis arvensis Linn.	1	2	6	8	6	9	9	5	2	2	1	.	9	12	12	18	51
Veronica serpyllifolia Linn.	19	15	9	11	4	3	.	3	.	2	1	.	6	6	7	48	67
V. hederaefolia Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Rhinanthus Crista-galli Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Prunella vulgaris Linn.	6	8	2	2	.	1	.	.	.	.	.	1	2	4	7	7	20
Mentha aquatica Linn.	.	3	2	.	.	1	.	.	.	.	.	.	1	1	.	4	6
Galeopsis Tetrahit Linn.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	2	2
Lamium purpureum Linn.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	1
Plantago lanceolata Linn.	5	.	.	.	.	.	.	.	.	.	.	.	1	4	.	.	5
P. major Linn.	19	30	22	6	10	3	1	3	1	.	.	.	8	6	27	54	95
Polygonum aviculare Linn.	.	.	.	1	.	1	.	.	.	.	.	.	1	.	.	1	2
P. Convolvulus Linn.	.	.	1	1	2	.	.	.	.	.	.	.	2	2	.	.	4
Rumex obtusifolius Linn.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	2	2
R. acetosa Linn.	.	.	.	2	.	.	.	.	.	.	.	.	.	2	.	.	2
R. acetosella Linn.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	1
Euphorbia Helioscopia Linn.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	1
Urtica dioica Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Juncus communis Mey.	5	2	.	.	2	.	.	.	1	.	.	.	3	.	5	2	10
J. articulatus Linn.	1	.	2	.	.	.	.	.	.	.	.	.	1	.	.	2	3
J. bufonius Linn.	.	.	1	2	1	.	.	1	1	.	.	.	.	.	3	3	6
Total	327	430	192	133	79	65	40	27	14	13	6	3					1329
GRASSES:																	
Anthoxanthum odoratum Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Agrostis spp.	8	.	2	4	.	.	.	.	.	.	.	.	7	4	3	.	14
Holcus lanatus Linn.	19	3	2	.	.	.	.	.	.	.	.	.	.	2	20	2	24
Cynosurus cristatus Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Poa trivialis Linn.	48	9	16	.	.	.	1	.	1	1	.	.	17	11	43	5	76
P. annua Linn.	35	21	14	1	3	2	.	.	.	.	.	.	31	2	10	33	76
P. pratensis Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Festuca rubra Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Lolium perenne Linn.	.	2	.	.	.	.	.	.	.	.	.	.	2	.	.	.	2
Total	113	36	34	5	3	2	1	.	1	1	.	.					196
LEGUMES:																	
Trifolium repens Linn.	3	8	1	.	1	.	.	1	1	1	.	1	6	3	6	2	17
T. minus Sm.	.	1	.	.	.	.	1	.	.	.	.	.	1	.	.	1	2
Total	3	9	1	.	1	.	1	1	1	1	.	1					19

Delayed germination again occurred with *Sagina procumbens*. In the case of charlock, on the contrary, germination was completed soon after the exposure of the soil samples; this may be further indication that the seeds had been buried in the soil for a considerable time, since in this plant natural dormancy of seeds is normally found.

(3) *Capel Dewi, Lovesgrove, Fron Capel Dewi.*

This field has been maintained as pasture for 24 years; the sward was analysed as follows: *Lolium perenne* 8½, *Cynosurus cristatus* 10½, *Poa tri-*

vialis 13½, *P. annua* 1, *Dactylis glomerata*—trace, *Festuca rubra* 13, *Holcus lanatus* 28½, *Agrostis* spp. 20, *Trifolium repens* 4, and *Cerastium vulgatum*, *Taraxacum officinale*, *Prunella vulgaris* and *Ranunculus* spp. together making 1.

Table X. *Lovesgrove.*

Profiles *a*, *b*, *c* and *d*. Depth of all profiles 12 in.

	Depths in inches												Total for each profile				Aggregate total
MISCELLANEOUS PLANTS:	1	2	3	4	5	6	7	8	9	10	11	12	*a*	*b*	*c*	*d*	
Ranunculus repens Linn.	7	41	64	61	13	10	13	8	1	.	3	2	26	56	53	88	223
Fumaria officinalis Linn.	.	1	2	3	1	.	.	3	5	1	1	1	1	10	3	4	18
Brassica Sinapis Visiani	.	.	.	.	.	1	2	.	1	.	.	.	2	.	1	1	4
Viola arvensis Murr.	.	1	.	.	.	1	.	.	.	.	.	.	2	.	.	.	2
Sagina procumbens Linn.	12	20	32	19	8	9	17	4	6	1	2	1	50	27	29	25	131
Cerastium vulgatum Linn.	28	55	34	15	9	2	2	3	1	.	3	5	52	21	69	15	157
Stellaria media Cyrill.	.	1	1	.	1	1	.	5	.	.	.	.	.	8	.	1	9
Hypericum humifusum Linn.	.	.	2	.	3	1	1	2	.	.	1	2	3	3	4	2	12
Alchemilla arvensis Scop.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	1
Epilobium montanum Linn.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	1
Taraxacum officinale Linn.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	3	3
Sonchus oleraceus Linn.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	1
Bellis perennis Linn.	7	8	7	4	1	1	1	.	.	.	1	1	15	2	10	4	31
Leontodon hispidus Linn.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	1
Chrysanthemum Leucanthemum Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
C. segetum Linn.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	1
Carduus arvensis Robs.	.	.	2	2	.	.	.	2	.	2	2	4	7	7	.	.	14
Senecio vulgaris Linn.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	1
Anagallis arvensis Linn.	.	.	3	.	7	3	4	1	.	.	.	.	3	8	2	5	18
Veronica serpyllifolia Linn.	11	20	36	20	17	13	3	5	.	3	4	3	46	36	33	20	135
Prunella vulgaris Linn.	2	2	22	8	2	7	2	.	.	.	.	.	13	3	21	8	45
Galeopsis Tetrahit Linn.	.	.	.	2	.	1	.	.	.	.	.	.	.	.	3	.	3
Plantago lanceolata Linn.	1	.	1	.	.	.	.	.	.	.	.	.	1	1	.	.	2
P. major Linn.	5	6	10	8	2	1	2	.	.	.	1	.	10	3	9	13	35
Chenopodium album Linn.	.	1	.	6	12	3	5	6	2	.	.	.	9	3	17	6	35
Polygonum aviculare Linn.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	1
P. convolvulus Linn.	.	.	1	1	1	1	2	.	.	.	.	.	2	1	3	.	6
Rumex acetosa Linn.	.	.	1	1	.	.	.	.	.	.	.	.	1	1	.	.	2
Euphorbia Helioscopia Linn.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	2	2
Urtica dioica Linn.	.	.	.	.	.	.	1	.	.	.		.	1	.	.	.	1
Juncus communis Mey.	1	.	.	.	.	1	1	.	.	1	.	.	1	.	1	2	4
J. bufonius Linn.	.	1	.	2	.	1	.	1	.	.	.	.	.	.	3	2	5
Total	75	158	220	153	78	59	56	40	17	8	22	19					905
GRASSES:																	
Agrostis spp.	22	18	15	2	.	.	2	.	.	.	.	1	11	9	12	28	60
Holcus lanatus Linn.	51	15	8	2	1	2	1	.	.	1	.	2	22	25	27	9	83
Cynosurus cristatus Linn.	4	1	.	.	.	.	.	.	.	.	.	.	.	1	2	2	5
Dactylis glomerata Linn.	.	3	2	.	.	.	.	.	.	.	.	.	.	.	5	.	5
Poa trivialis Linn.	70	31	40	26	10	5	5	1	.	1	2	3	49	49	76	20	194
P. annua Linn.	19	7	25	15	10	9	2	7	5	4	2	3	47	26	30	5	108
Festuca rubra Linn.	30	10	15	.	.	.	.	.	.	.	.	.	12	33	10	.	55
Lolium perenne Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Total	197	85	105	45	21	16	10	8	5	6	4	9					511
LEGUMES:																	
Trifolium repens Linn.	6	5	18	7	2	1	.	1	1	.	.	2	12	21	2	8	43

The seedlings growing out of the soil from this field (Table X) show a general resemblance to those of the previous example, but the number of dicotyledonous seedlings is much less and that of grasses larger. Almost half the former species are characteristic of arable land and these are again buried some depth in the soil. There is here also, therefore, the suggestion that seeds have remained viable since the time when the cultivation was changed; the fact, however, that none of the typical pasture seeds has its greatest density of distribution in the first inch of soil, shows that there is some danger in basing any assumption on the situation of seeds.

With the usual exceptions of *Lolium perenne* and *Cynosurus cristatus*, grass seeds are well represented in the soil of this pasture, notable among them being those of *Festuca rubra*. Having regard, however, to its prominence in the sward, the seedlings of *Agrostis* are fewer in number than would have been expected from the results obtained with other fields.

(4) *Waun-fawr, Frongôch, Brook Field.*

This field has been improved by drainage and cultivation from the condition described above under Marsh; it was formerly in arable cultivation, but the present sward has been undisturbed for 22 years. The composition of the latter was as follows: *Cynosurus cristatus* 16½, *Poa trivialis* 12, *Festuca rubra* 1, *Holcus lanatus* 28½, *Agrostis* spp. 15½, *Anthoxanthum odoratum* 2½, *Triodia decumbens* 1, *Carex* spp. 15½, *Juncus* spp. 3½, *Trifolium repens* 2, traces of *Poa annua*, *Luzula campestris*, *Lotus corniculatus* and *Trifolium minus*, and *Rumex acetosa*, *Bellis perennis* and *Centaurea nigra* together making 2. This analysis shows a decided similarity as regards species with that obtained from the Marsh, but there is here a greater amount of *Cynosurus cristatus*, *Poa trivialis* and *Carex*, and less of *Holcus lanatus*, *Agrostis* and *Juncus*.

It will be seen from Table XI that the number of seedlings is greater in this case than in that of any other example, this being due possibly to the field having been neglected for some years and grazed lightly. The species, however, show a very general agreement with those derived from the Marsh (Table IV), the only notable differences in the present instance being the smaller numbers of seedlings of *Lotus corniculatus* and *Agrostis*, the greater numbers of *Ranunculus repens*, *Trifolium repens*, *Holcus lanatus* and *Poa trivialis* and the occurrence of *Senecio Jacobaea* and *Cynosurus cristatus*. The number of seedlings of the latter is not large, but it is greater than in the case of any other field, this being, however, the only dissimilarity from the representation of grass species in the other fields. Traces of the period of arable management are meagre, but the occurrence of *Spergula arvensis* and *Polygonum Persicaria* are probably to be regarded as such. Delayed germination has again been shown by species already noted and also by *Cerastium vulgatum*.

With this field and also in the case of Barn Field described earlier, it would seem that any treatment which exposes bare soil would be liable to produce a deterioration of the sward.

(5) *Llanfarian, Pen-y-graig, Cae Ysgubor.*

The sward of this example was sown 6 years ago: it is, however, exceptionally close and the composition particularly good. The latter gave the following analysis: *Lolium perenne* 50, *Cynosurus cristatus* 3, *Poa trivialis* 24, *P. annua* 2½, *Holcus lanatus* 2, *Agrostis vulgaris* 2½, *Trifolium repens* 15, and

Cerastium vulgatum, *Bellis perennis*, *Plantago lanceolata*, *Rumex obtusifolius*, *Achillea Millefolium* and *Ranunculus* spp. together making 1.

Table XI. *Brook Field*.

Profiles *a*, *b*, *c* and *d*. Depth of all profiles 12 in.

	Depths in inches												Total for each profile				Aggregate total
	1	2	3	4	5	6	7	8	9	10	11	12	*a*	*b*	*c*	*d*	
MISCELLANEOUS PLANTS:																	
Ranunculus repens Linn.	709	746	639	138	43	16	11	3	3	4	3	.	309	695	557	754	2315
R. Flammula Linn.	102	191	41	13	18	15	21	31	7	14	3	1	71	242	20	124	457
Cardamine hirsuta Linn.	9	.	1	.	.	.	.	.	.	.	.	.	1	.	.	9	10
Polygala vulgaris Linn.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	4	4
Spergula arvensis Linn.	.	6	2	.	.	.	1	.	.	.	.	.	9	.	.	.	9
Sagina procumbens Linn.	32	41	21	5	4	8	.	.	.	.	1	.	28	78	4	2	112
Cerastium vulgatum Linn.	121	27	13	.	2	1	.	.	.	.	.	.	28	40	35	61	164
Stellaria media Cyrill.	92	1	1	.	.	.	.	.	.	.	.	.	.	.	1	93	94
S. uliginosa Murr.	53	13	10	6	2	4	2	2	.	.	.	.	2	.	3	87	92
Montia fontana Linn.	.	2	.	.	.	.	.	.	.	.	.	.	.	2	.	.	2
Potentilla erecta Hampi.	1	.	1	.	2	2	.	2	2	1	1	.	1	1	4	6	12
Epilobium montanum Linn.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	5
Taraxacum officinale Web.	29	30	.	.	.	.	.	.	.	1	.	.	7	53	.	.	60
Gnaphalium uliginosum Linn.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	2	2
Sonchus oleraceus Linn.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	1
Senecio Jacobaea Linn.	99	76	27	19	11	2	2	1	3	.	.	.	71	72	7	90	240
Bellis perennis Linn.	29	12	21	.	.	.	.	.	.	.	.	.	4	50	5	3	62
Leontodon hispidus Linn.	11	8	.	.	.	.	.	.	.	.	.	.	.	16	3	.	19
Chrysanthemum Leucanthemum Linn.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	1
C. segetum Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Carduus palustris Linn.	1	1	1	.	.	.	.	.	.	.	.	.	.	1	2	.	3
Anagallis arvensis Linn.	.	1	.	1	1	.	.	.	.	.	.	.	1	.	.	2	3
A. tenella Linn.	1	.	7	11	8	23	13	4	.	.	.	.	24	3	36	4	67
Veronica serpyllifolia Linn.	4	9	17	16	6	4	1	1	.	.	.	.	16	27	13	2	58
Prunella vulgaris Linn.	19	24	4	.	.	.	.	.	.	.	.	.	11	33	3	.	47
Mentha aquatica Linn.	10	2	.	8	.	.	.	.	.	.	.	.	8	12	.	.	20
Scutellaria minor Linn.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	8
Plantago lanceolata Linn.	16	13	6	.	1	1	.	.	.	1	.	.	16	21	.	1	38
P. major Linn.	16	40	75	41	19	8	2	.	1	1	.	.	21	121	58	3	203
Polygonum aviculare Linn.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	1
P. Persicaria Linn.	1	1	1	5	4	6	1	1	.	.	.	.	2	1	4	13	20
Rumex obtusifolius Linn.	1	1	2	.	.	.	.	.	.	.	.	.	2	1	.	1	4
R. acetosa Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Luzula campestris Br.	.	1	.	.	.	.	1	1	.	.	.	.	2	.	1	.	3
Juncus communis Mey.	119	104	83	70	50	57	17	4	2	1	.	.	231	15	108	153	507
J. articulatus Linn.	25	12	8	13	6	14	10	2	1	.	.	.	28	22	5	36	91
J. bufonius Linn.	24	57	43	47	34	40	36	19	5	8	1	.	107	12	69	126	314
J. triglumis Linn.	.	1	.	1	.	.	.	.	.	.	.	.	1	.	1	.	2
J. bulbosus Linn.	.	.	.	4	.	3	2	.	.	.	.	.	4	.	1	4	9
J. squarrosus Linn.	.	.	1	.	1	.	1	.	.	.	.	.	.	.	3	.	3
Scirpus setaceus Linn.	5	26	13	24	27	27	26	3	.	1	.	.	21	28	57	46	152
Carex spp.	157	108	43	42	28	51	46	28	10	4	2	.	204	97	147	71	519
Total	1700	1560	1081	465	267	283	194	103	34	36	11	1					5735
GRASSES:																	
Anthoxanthum odoratum Linn.	26	21	.	.	.	.	.	.	.	.	.	.	2	14	29	2	47
Agrostis spp.	19	9	7	13	11	7	4	3	2	4	.	.	33	25	12	9	79
Holcus lanatus Linn.	119	58	3	2	.	.	.	.	.	.	.	.	8	51	87	36	182
Triodia decumbens Beauv.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	1
Cynosurus cristatus Linn.	29	5	.	.	.	.	.	.	.	.	.	.	4	10	17	3	34
Poa trivialis Linn.	153	54	25	8	2	.	2	2	.	.	1	.	28	33	90	96	247
P. annua Linn.	8	7	4	4	3	1	3	.	1	.	.	.	2	12	13	4	31
Glyceria fluitans Sm.	1	2	.	1	.	.	.	.	.	.	.	.	.	4	.	.	4
Festuca rubra Linn.	2	.	.	1	2	1	3	.	.	.	.	.	3	3	.	3	9
Lolium perenne Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Total	358	156	39	30	18	9	12	5	3	4	1	.					635
LEGUMES:																	
Trifolium pratense Linn.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	1
T. repens Linn.	27	40	29	10	5	1	3	2	.	.	2	.	37	45	21	16	119
Lotus corniculatus Linn.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	1
Lathyrus pratensis Linn.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	3
Total	30	40	29	12	5	1	3	2	.	.	2	.					124

Table XII. *Llanfarian.*

Profiles *a*, *b* and *c*. Depths of profiles: *a*, 12 in.; *b*, 10 in.; *c*, 11 in.

	Depths in inches												Total for each profile			Aggregate total
MISCELLANEOUS PLANTS:	1	2	3	4	5	6	7	8	9	10	11	12	*a*	*b*	*c*	
Ranunculus repens Linn.	87	11	5	9	4	18	3	2	2	.	1	.	31	5	106	142
Fumaria officinalis Linn.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	1
Brassica Sinapis Visiani	3	14	5	13	44	2	8	.	2	.	.	.	15	26	50	91
B. campestris Linn.	.	.	.	1	6	.	1	.	.	.	.	.	.	3	5	8
Viola arvensis Murr.	3	2	2	7	2	6	2	2	1	2	.	.	19	5	5	29
Spergula arvensis Linn.	9	4	1	.	2	1	.	.	.	.	.	.	14	2	1	17
Sagina procumbens Linn.	15	22	18	14	16	14	10	5	4	.	3	.	26	60	35	121
Cerastium vulgatum Linn.	2	1	.	.	.	.	1	2	1	.	.	.	.	.	7	7
Stellaria media Cyrill.	2	2	1	2	4	.	.	8	1	.	.	.	9	4	7	20
Hypericum humifusum Linn.	.	.	.	.	.	.	.	.	1	.	.	.	.		1	1
Geranium molle Linn.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	1
Alchemilla arvensis Scop.	1	60	1	4	6	1	29	.	.	1	.	.	2	97	4	103
Conopodium denudatum Koch.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	1
Anthemis Cotula Linn.	.	2	.	2	2	.	.	.	.	.	.	.	.	.	6	6
Taraxacum officinale Web.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1
Sonchus oleraceus Linn.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	1
Bellis perennis Linn.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Chrysanthemum segetum Linn.	3	4	1	5	9	7	.	.	.	.	.	.	5	24	.	29
Lapsana communis Linn.	2	4	1	6	6	20	3	1	1	.	.	.	22	9	13	44
Anagallis arvensis Linn.	6	6	13	5	8	9	10	3	2	2	1	.	14	26	25	65
Veronica serpyllifolia Linn.	5	2	3	4	1	1	1	.	1	1	.	.	4	9	6	19
Prunella vulgaris Linn.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2
Galeopsis Tetrahit Linn.	.	.	2	2	5	10	3	.	.	.	.	.	14	2	6	22
Plantago major Linn.	1	2	6	3	2	2	4	4	4	2	.	.	3	7	20	30
Chenopodium album Linn.	.	1	2	4	4	5	1	.	1	.	.	.	5	8	5	18
Polygonum aviculare Linn.	.	4	3	6	3	3	2	.	.	1	.	.	8	7	7	22
P. Persicaria Linn.	1	1	.	1	1	2	3	3	.	.	1	1	6	4	4	14
P. Convolvulus Linn.	.	.	.	3	4	1	.	1	.	.	.	.	1	3	5	9
P. Bistorta Linn.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	1
Rumex obtusifolius Linn.	1	.	.	.	1	.	.	.	.	.	.	.	1	.	1	2
R. acetosa Linn.	5	22	15	.	22	12	6	2	4	.	.	.	29	5	54	88
R. acetosella Linn.	.	1	.	.	3	.	2	.	2	.	.	.	4	.	4	8
R. crispus Linn.	1	.	.	.	.	.	.	.	2	.	.	.	.	.	3	3
Euphorbia Helioscopia Linn.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	2	2
Juncus communis Mey.	1	.	.	.	1	.	.	.	.	1	.	.	1	.	2	3
J. bufonius Linn.	.	1	.	.	.	1	.	.	1	.	.	.	2	1	.	3
Total	150	167	80	93	158	115	89	33	31	11	7	1				935
GRASSES:																
Agrostis spp.	5	3	1	1	2	1	.	.	.	.	.	.	1	4	8	13
Holcus lanatus Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Dactylis glomerata Linn.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	2	2
Poa trivialis Linn.	22	9	7	12	5	1	6	4	2	3	4	.	10	13	52	75
P. annua Linn.	108	93	47	36	31	20	20	19	16	8	11	.	20	11	378	409
Agropyrum repens Beauv.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	1
Total	136	108	55	49	38	22	26	23	18	11	15	.				501
LEGUMES:																
Trifolium repens Linn.	3	6	4	6	2	4	7	2	1	.	.	.	11	15	9	35

The results here (cf. Table XII) show abundant evidence of seeds remaining viable in the soil since the time when the field was arable. Species characteristic of pasture are, in fact, very poorly represented, and the grass seedlings present are almost entirely Poas which occur under both forms of management. This would seem to show that many weed seeds are destroyed by some means so that the stock of seeds in the soil is only slowly built up. It is clear that were the existing sward to be destroyed the flora of this field would immediately become typical of arable land.

Delayed germination occurred markedly with *Sagina procumbens* and *Alchemilla arvensis* and to a slight extent in *Ranunculus repens*, *Poa annua* and *Trifolium repens*.

D. *Fields annually put up to hay.*

(1) *Wallog, Rhoscellan Fawr, Caellwyndu.*

This field has not been ploughed for 68 years. The percentage tiller composition of the herbage was as follows: *Lolium perenne* 2½, *Dactylis glomerata* 17, *Cynosurus cristatus* 8, *Alopecurus pratensis* 1, *Poa trivialis* 17, *Festuca rubra* 20, *Holcus lanatus* 20½, *Anthoxanthum odoratum* 1½, *Agrostis* spp. 9, *Luzula campestris*—a trace, *Trifolium repens* 1½, *T. pratense* 1, and *Plantago lanceolata, Rumex acetosa, Prunella vulgaris, Cerastium vulgatum, Achillea Millefolium* and *Ranunculus* spp. together making 1.

The results given in Table XIII are hardly what would have been expected from a field that has been under grass so long. The absence of grazing during the spring seems chiefly to have favoured seed production in such weeds as sorrel and daisy, and the representation of the grass species in no way differs from that in grazed fields. Several species characteristic of arable land occur, and in most cases the seeds are some distance within the soil. It is noticeable, however, that seeds of *Fumaria officinalis, Chrysanthemum segetum* and *Chenopodium album* occur in the first inch, suggesting that these are of recent introduction.

Delayed germination again took place in species previously recorded.

(2) *Waun-fawr, Erwgoch, Cae-tu-ôl-ty.*

The herbage of this example was analysed as follows: *Lolium perenne* 20; *Dactylis glomerata* 2, *Phleum pratense* 3, *Cynosurus cristatus* 12½, *Poa trivialis* 20½, *P. annua* 2, *Holcus lanatus* 11½, *Agrostis* spp. 2½, *Festuca rubra*—a trace, *Anthoxanthum odoratum* 2, *Trifolium repens* 21½, *T. pratense* ½, *T. minus*—a trace and 2 of weeds (*Bellis perennis, Prunella vulgaris, Plantago lanceolata, Taraxacum officinale, Cerastium vulgatum, Rumex obtusifolius, R. acetosa, Vicia sativa* and *Ranunculus* spp.). The field has been under grass only for 8 years and, as in the case of Llanfarian, arable weeds are present in the soil in considerable quantities (cf. Table XIV); the number of seedlings of grassland weeds is here, however, larger. The position in regard to grasses is not different from that found in pasture, except that the number of *Poa* seedlings is unusually high; many of these have probably arisen from seeds which entered the ground when the field was arable.

Evidence of natural dormancy in the seeds of species already recorded was again obtained.

GENERAL OBSERVATIONS AND DISCUSSION.

The most remarkable feature of these results is the extreme variation shown by the different species of plants in respect of the numbers of viable seeds which are in the soil; correlated with this is the complete absence of any close association between the surface vegetation and the seed flora of the soil beneath.

Table XIII. *Wallog.*

Profiles *a*, *b*, *c* and *d*. Depths of profiles: *a*, 11 in.; *b*, 12 in.; *c*, 10 in.; *d*, 11 in.

	Depths in inches												Total for each profile				Aggregate total
	1	2	3	4	5	6	7	8	9	10	11	12	*a*	*b*	*c*	*d*	
MISCELLANEOUS PLANTS:																	
Ranunculus repens Linn.	222	52	21	17	8	5	7	.	6	5	4	.	100	58	51	138	347
R. Flammula Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Fumaria officinalis Linn.	196	3	.	2	.	4	.	1	.	.	.	.	93	48	55	10	206
Viola arvensis Linn.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	1
Sagina procumbens Linn.	2	1	22	.	.	.	.	.	.	.	.	.	.	2	23	.	25
Cerastium vulgatum Linn.	30	21	24	13	7	6	5	2	1	5	1	.	66	28	6	15	115
Stellaria media Cyrill.	.	.	1	3	.	.	.	.	1	.	.	.	.	4	1	.	5
Hypericum humifusum Linn.	.	2	.	2	2	2	.	3	2	1	.	.	3	2	8	1	14
Geranium molle Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Potentilla reptans Linn.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	1
Alchemilla arvensis Scop.	.	.	4	.	.	1	.	.	.	.	.	.	.	.	3	2	5
Conopodium denudatum Koch.	.	.	2	2	.	.	.	.	.	.	.	.	4	.	.	.	4
Taraxacum officinale Web.	27	7	2	1	.	.	2	1	.	.	1	.	9	6	22	4	41
Sonchus oleraceus Linn.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Bellis perennis Linn.	161	58	10	4	7	.	3	5	.	2	1	.	140	16	74	21	251
Leontodon hispidus Linn.	2	.	1	.	.	.	.	.	.	.	.	.	1	.	2	.	3
Chrysanthemum Leucanthemum Linn.	17	5	6	3	7	3	4	3	.	.	2	.	24	12	6	8	50
C. segetum Linn.	3	8	.	.	.	.	.	.	.	.	.	.	.	5	3	3	11
Lapsana communis Linn.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	1
Anagallis arvensis Linn	.	2	11	3	23	4	5	2	3	1	.	1	32	2	6	15	55
A. tenella Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Veronica serpyllifolia Linn.	2	1	5	6	.	.	1	.	2	.	.	.	1	10	5	1	17
Digitalis purpurea Linn.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	1
Euphrasia officinalis Linn.	5	2	2	.	.	.	.	.	.	.	.	.	.	.	1	8	9
Rhinanthus Crista-galli Linn.	.	1	.	.	.	.	2	.	.	.	.	.	2	.	.	1	3
Prunella vulgaris Linn.	.	4	.	.	.	.	.	.	.	.	1	.	2	1	1	1	5
Mentha aquatica Linn.	.	.	1	1	.	1	1	.	1	.	.	.	.	.	1	4	5
Galeopsis Tetrahit Linn.	.	.	.	1	1	1	.	.	.	.	.	.	.	.	3	.	3
Stachys arvensis Linn.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	1
Plantago lanceolata Linn.	4	3	2	.	.	.	1	.	.	.	.	.	7	.	1	2	10
P. major Linn.	1	8	2	1	.	.	.	.	.	1	.	.	1	7	1	4	13
Chenopodium album Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Polygonum aviculare Linn.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	1
P. Persicaria Linn.	.	.	.	.	1	.	1	.	.	.	.	.	1	1	.	.	2
Rumex acetosa Linn.	170	10	5	4	2	4	4	1	4	2	.	.	77	86	17	26	206
Euphorbia Helioscopia Linn.	.	.	2	.	1	1	.	.	.	.	.	.	.	.	3	1	4
Parietaria officinalis Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Luzula campestris Br.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	2	2
Juncus communis Mey.	3	3	2	3	2	1	.	.	2	.	.	.	2	9	2	3	16
J. articulatus Linn.	2	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	2
J. bufonius Linn.	1	5	3	5	1	2	.	1	2	2	1	.	4	16	3	.	23
Carex spp.	2	.	2	.	1	2	3	.	1	2	1	1	4	6	2	3	15
Total	852	200	131	73	64	40	40	19	25	21	12	2					1479
GRASSES:																	
Anthoxanthum odoratum Linn.	9	1	.	.	.	.	.	.	.	.	.	.	2	5	2	1	10
Agrostis spp.	19	8	1	1	1	2	.	.	.	.	.	.	1	9	11	11	32
Holcus lanatus Linn.	92	14	7	1	.	.	1	1	.	1	.	.	46	43	9	19	117
Triodia decumbens Beauv.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1
Cynosurus cristatus Linn.	6	3	.	.	.	.	.	.	.	.		.	2	2	3	2	9
Dactylis glomerata Linn.	19	1	2	.	.	.	.	.	.	.	.	.	3	12	5	2	22
Poa trivialis Linn.	69	12	8	11	7	1	11	1	3	2	1	1	13	83	12	19	127
P. annua Linn.	10	5	2	1	.	1	.	.	.	1	1	.	6	8	5	2	21
Festuca rubra Linn.	3	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	3
Total	227	45	20	14	8	4	12	2	3	4	2	1					342
LEGUMES:																	
Trifolium pratense Linn.	5	.	.	.	1	.	.	2	1	.	.	.	2	.	1	6	9
T. repens Linn.	2	7	18	9	5	2	.	6	1	3	2	.	5	32	9	9	55
T. minus Linn.	.	.	1	.	.	.	.	1	.	.	.	.	1	1	.	.	2
Total	7	7	19	9	6	2	.	9	2	3	2	.					66

An important example of the latter is the large numbers of *Calluna vulgaris* and *Erica cinerea* which occur in all the upland areas, although, with the exception of one area, these plants constitute a very low proportion of the

Table XIV. *Erwgoch.*

Profiles *a*, *b*, *c* and *d*. Depths of profiles: *a*, 12 in.; *b*, 12 in.; *c*, 9 in.; *d*, 9 in.

	Depths in inches												Total for each profile				Aggregate total
MISCELLANEOUS PLANTS:	1	2	3	4	5	6	7	8	9	10	11	12	*a*	*b*	*c*	*d*	
Ranunculus repens Linn.	41	9	2	8	16	4	5	6	3	1	1	1	6	50	23	18	97
Fumaria officinalis Linn.	3	.	1	1	.	.	1	1	2	1	.	.	2	3	9	.	24
Brassica Sinapis Visiani	44	14	.	.	9	15	20	.	.	.	.	.	.	7	93	2	102
B. campestris Linn.	3	.	5	15	.	1	.	.	1	.	.	.	1	3	18	3	25
Viola arvensis Murr.	5	2	2	5	4	4	.	.	.	.	.	.	1	11	8	2	22
Spergula arvensis Linn.	3	10	1	3	.	.	.	.	.	.	.	.	13	1	1	2	17
Sagina procumbens Linn	21	36	57	60	54	121	75	40	10	7	.	2	20	318	112	33	483
Cerastium vulgatum Linn.	44	14	8	3	4	6	7	1	2	.	.	2	12	41	21	17	91
Stellaria media Cyrill.	.	4	9	10	13	16	2	.	.	1	.	.	5	4	7	39	55
Hypericum humifusum Linn.	.	.	1	.	1	3	2	4	.	.	1	.	.	4	6	2	12
Potentilla reptans Linn.	.	.	1	2	.	.	.	.	.	.	.	.	.	3	.	.	3
Alchemilla arvensis Scop.	15	8	3	4	3	5	4	2	1	.	.	.	.	26	.	19	45
Taraxacum officinale Web.	10	4	.	.	1	.	.	.	.	.	.	.	5	.	5	5	15
Gnaphalium uliginosum Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Sonchus oleraceus Linn.	.	2	.	1	.	.	1	.	.	.	.	.	1	3	.	.	4
Bellis perennis Linn.	210	44	38	10	7	4	6	5	3	.	.	.	52	52	155	68	327
Leontodon hispidus Linn.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Chrysanthemum Leucanthemum Linn.	8	.	.	2	2	1	3	17	1	2	.	.	4	3	26	3	36
C. segetum Linn.	.	.	.	.	.	2	2	1	.	.	.	.	1	.	1	3	5
Lapsana communis Linn.	1	.	2	1	.	.	.	1	.	.	.	.	.	5	.	.	5
Anagallis arvensis Linn.	6	7	11	16	16	17	19	13	6	.	.	.	43	7	49	12	111
Veronica serpyllifolia Linn.	24	30	21	25	24	16	19	7	3	1	.	.	16	44	81	29	170
V. hederaefolia Linn.	5	1	.	.	.	1	.	.	.	.	.	.	2	2	3	.	7
Pedicularis sylvatica Linn.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Prunella vulgaris Linn.	3	7	.	3	5	3	2	1	.	.	.	.	8	4	7	5	24
Galeopsis Tetrahit Linn.	3	2	1	.	4	3	8	1	.	.	.	.	8	.	10	4	22
Stachys arvensis Linn.	1	.	.	.	1	.	1	3	1	.	.	.	3	.	3	1	7
Plantago lanceolata Linn.	12	1	1	.	1	.	.	1	.	.	.	.	8	2	.	6	16
P. major Linn.	7	6	10	4	12	3	2	1	.	.	.	.	18	7	4	16	45
Chenopodium album Linn.	8	20	23	22	20	10	6	2	1	.	.	.	39	24	27	22	112
Polygonum aviculare Linn.	1	2	2	1	.	.	.	.	.	.	.	.	3	2	1	.	6
P. Persicaria Linn.	2	7	1	1	2	.	.	.	.	.	.	.	3	2	3	5	13
P. Convolvulus Linn.	4	7	4	3	4	.	1	.	.	.	.	.	7	1	3	12	23
Rumex obtusifolius Linn.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	1
R. acetosa Linn.	19	5	5	5	1	1	.	.	.	.	.	.	2	.	33	1	36
Euphorbia Helioscopia Linn.	.	.	.	.	1	.	1	.	.	.	.	.	2	.	.	.	2
Urtica dioica Linn.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	1
Juncus communis Mey.	4	2	4	8	.	2	1	2	2	.	.	.	8	4	1	12	25
J. bufonius Linn.	2	5	5	5	1	1	5	.	.	1	.	.	6	10	4	5	25
J. bulbosus Linn.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	1
Carex spp.	2	.	.	.	.	.	.	.	.	.	.	1	1	1	.	1	3
Total	512	250	219	219	207	239	193	109	37	14	2	6					2007
GRASSES:																	
Anthoxanthum odoratum Linn.	2	.	.	1	.	.	.	.	.	.	.	.	.	.	.	3	3
Phleum pratense Linn.	1	.	.	1	.	.	.	.	.	.	.	.	.	1	.	1	2
Agrostis spp.	11	15	20	18	22	9	6	1	1	1	.	.	8	18	46	32	104
Holcus lanatus Linn.	18	2	.	.	.	.	1	.	.	.	.	.	8	3	8	2	21
Dactylis glomerata Linn.	4	.	.	.	1	.	.	.	.	.	.	.	.	1	1	3	5
Poa trivialis Linn.	73	6	6	5	5	11	4	4	.	1	.	.	21	37	24	33	115
P. annua Linn.	89	37	12	14	13	14	17	7	2	1	1	1	5	158	12	33	208
Lolium perenne Linn.	3	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	3
Total	201	60	38	39	41	34	28	12	3	3	1	1					461
LEGUMES:																	
Trifolium pratense Linn.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
T. repens Linn.	5	9	4	8	5	5	10	10	5	1	2	.	10	24	17	13	64
T. minus Sm.	57	8	10	6	1	2	8	2	.	1	.	.	79	8	5	3	95
Lotus corniculatus Linn.	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	2
Total	64	18	14	14	6	7	18	12	5	2	2	.					162

swards. The disparity is so extreme that there must clearly be taking place continually year by year, over these areas, a very high mortality in successive crops of *Calluna* and *Erica* seedlings, since some exposure of soil must always be occurring. There are two possible explanations of this; either (1) the conditions have for a long period of time been such as to stabilise the proportions of *Calluna* and *Erica* relative to the grasses at a small value, or (2) the grasses are in process of replacing heather over these areas. The latter hypothesis is felt to be by far the more probably correct.

A comparative examination of the occurrence and number of seedlings of the different plants shows the representation of the grasses to be astonishingly low considering that in almost all the areas examined these plants are dominant in the vegetation and have opportunity to develop seeds. It is clear that most grasses depend entirely on vegetative reproduction in maintaining their occupation of the ground (though not probably in the colonisation of other areas), and hence the plants found in pastures must be of very great age. (Confirmatory evidence of this is the perpetuation of grasses on lawns under conditions which inhibit completely the development of seeds.) There are, however, four possible exceptions to this behaviour in the cases of *Holcus lanatus*, *Poa trivialis*, *P. annua* and *Agrostis* spp.; with each of these species the density of seeds in the first inch of soil is in some fields equivalent to more than 1 lb. of viable seed per acre (which is a considerable seed rate in farming practice). It is easy to understand, therefore, why fields sown with more desirable sorts of grasses quickly revert in some cases to pasture dominated by *Agrostis* and *Holcus*. This must partly be due, also, to the absence of replenishment from seedlings of the former, and on both these accounts it is felt that the present results emphasise very definitely the importance of using vegetatively persistent strains of such grasses as *Lolium perenne* and *Dactylis glomerata* in practical agriculture.

A number of dicotyledons show evidence of behaving in a similar manner to most of the grasses, notably among them *Achillea Millefolium*, *Plantago lanceolata*, *Centaurea nigra* and possibly *Trifolium repens*; reproduction from seeds would also seem to be infrequent in *Scirpus caespitosus*.

It is possible in some of these cases, both of the grasses and of the dicotyledons, that this scarcity of viable seeds in the soil may be due in some measure to the seeds remaining on the surface of the soil and germinating without any period of dormancy; but it would seem very improbable that this can be the sole cause, since the several fields have been sampled at different times of the year. There must occur the destruction of large numbers of seeds by some agency. The latter would seem most probably to be birds and/or rodents, but there is no direct evidence in either case. Grass seeds are, in fact, conspicuously absent from the published data on the natural food of birds (5).

In the case of *Calluna vulgaris*, *Erica cinerea*, *Ranunculus repens*, *Sagina procumbens*, *Bellis perennis*, *Juncus communis*, *J. bufonius* and *Carex* spp., on the contrary, the number of seeds present in a viable condition in the soil is enormous and is often much out of proportion to the representation of these plants in the surface vegetation. It is significant that most of the species which show this behaviour have exceedingly small seeds.

There is a general tendency for the number of seeds of arable plants to diminish with increasing age of the pasture, and the evidence on the whole suggests that the seeds of these plants can retain their viability in the soil for very long periods (possibly 70 years), but there are also data which show that conclusive evidence on this matter cannot be obtained from such experiments as the present.

It is interesting to find that there is some differentiation of the species related to the occurrence of their seeds at considerable depths in the soil. The seeds of *Ranunculus repens, Anagallis arvensis, Poa trivialis, P. annua, Trifolium repens, Juncus* spp. and *Carex* spp. occur most frequently in the lower soil; except in the case of the upland areas, however, there is no species found in considerable numbers in the higher inches of soil which is not present also at a greater depth. The seeds of some species, more particularly the arable plants, show a tendency to occur some distance beneath the surface, and to be absent from the soil above.

A comparison of the total numbers of seedlings occurring in the different areas gives some indication that more seeds are present in a viable condition in water-logged soils, but the fields sampled are too small in number to establish definitely such an association.

The seasonal periodicity of germination, observed by Brenchley and Warington, in which a diminution is shown in the number of seedlings arising during late spring and summer, has not been found in the present work, except possibly in some arable species and in the case of *Alchemilla arvensis*, which has shown a tendency to germinate during autumn and winter. The other species have, in fact, appeared in greatest numbers in the spring and summer months. Nothing has suggested that this is anything other than an effect of the higher temperatures which prevail at that time. There would, therefore, appear to be a very interesting difference in this respect between plants characteristic of arable and of pasture soils. The seeds of arable species (particularly charlock) have usually germinated immediately after the exposure of the soil samples—a procedure intelligible on the assumption that the seeds have been in the soil for a considerable time. The same behaviour, also, is shown by most of the seeds of *Ranunculus repens* and *Holcus lanatus*.

The following species have been noted above as showing delayed germination (i.e. natural dormancy) in the seeds: *Calluna vulgaris, Erica cinerea, Galium saxatile, Anagallis tenella, Cerastium vulgatum, Bellis perennis, Gnaphalium uliginosum, Ranunculus repens, Alchemilla arvensis, Sagina procumbens, Epilobium montanum, Trifolium repens, T. minus, Carex* spp., *Juncus articulatus, J. communis, J. bufonius, J. bulbosus, J. triglumis, Scirpus setaceus, Poa trivialis* and *P. annua.*

SUMMARY.

An investigation into the occurrence of viable seeds in soils underlying pastures has provided evidence for the following statements.

1. At several upland areas a transition is taking place from a *Calluna* association to grassland.
2. Most species of grasses, possibly *Trifolium repens*, and some other dicotyledons perpetuate themselves in pastures chiefly by vegetative means.
3. In pastures which have formerly been under the plough, seeds of species characteristic of arable land occur, even after a period of 68 years.
4. Germination of the buried seeds is largely confined to the spring and summer months.
5. Delayed germination occurs in the seeds of many species of grassland plants.
6. In some areas, any cultivation which involves the exposure of bare soil is inadvisable, since it provides an opportunity for germination to seeds of rushes and other weeds which may be present in great numbers where the plants themselves are infrequent in the existing sward.

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THE DISTRIBUTION OF "CALCICOLE" AND "CALCIFUGE" SPECIES IN RELATION TO THE CONTENT OF THE SOIL IN CALCIUM CARBONATE AND EXCHANGEABLE CALCIUM, AND TO SOIL REACTION[1]

BY B. L. T. DE SILVA.

(*With six Figures in the Text.*)

CALCICOLOUS plants, or "calcicoles," are commonly defined as plants found growing in soils rich in calcium carbonate: calcifugous plants, or "calcifuges," as plants growing in soils deficient in or devoid of calcium carbonate, and at the same time acid in reaction. Little or no notice seems to have so far been taken of the fact that markedly "calcicolous" plants (i.e. plants which are characteristically luxuriant on highly calcareous soils), such as *Mercurialis perennis* and *Arum maculatum*, can and very often do flourish in soils in which there is no detectable amount of calcium carbonate.

The question then arises as to whether reaction alone is the determining factor, and if so what agent is responsible for preventing the normal rise of acidity of the soil with time.

Determinations were made of the calcium carbonate content, exchangeable calcium content, and soil reaction of various soils in which these and other plants were growing. Estimations of nitrates were also carried out, for two purposes: first, to see whether the nitrate content in any way affected the nature of the plant growth, and secondly, whether production of nitrates, i.e. the activity of the nitrifying bacteria themselves, can be correlated with any of the other factors considered. Nitrifying bacteria generally flourish in soils that are not, or are only slightly, acid, and which usually contain calcium carbonate. The nitrifying bacteria as a group are in fact usually themselves calcicolous plants. But a number of instances are known where nitrifying bacteria are found to be quite active in acid soils. Investigation was therefore made to see whether abundance of exchangeable calcium was in any way responsible for their activity in acid soils.

METHODS.

Determination of exchangeable calcium. The method adopted was a slight modification of the original method of Gedroiz (5). 10 gm. of air-dried soil were digested at 70° C. for 1 hour with 100 c.c. of normal ammonium chloride. The digested soil was allowed to stand for half an hour and then leached out with normal ammonium chloride in the usual way till 500 c.c. of "leachate" was obtained. The calcium in the leachate was determined by precipitating it as oxalate, decomposing the oxalate with standard permanganate. Where the soil contained calcium carbonate a correction for calcium directly dissolved by the ammonium chloride was made by determining the calcium in a second leaching of the soil.

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[1] Part of a thesis accepted for the degree of Master of Science in the University of London.

Degree of unsaturation of the soil (i.e. the amount of exchangeable hydrogen in the soil). Here the method adopted was in the main that originally suggested by Page and Williams (**11**) and later adopted by Turner (**19**). The exchangeable hydrogen is determined together with exchangeable calcium as the total saturation capacity. 10 gm. of the soil were mixed with an excess of pure precipitated calcium carbonate, and later stirred up with 100 c.c. of hot sodium chloride. The mixture was allowed to stand overnight. The soil was then leached with sodium chloride as usual and the calcium in the leachate determined. A correction was made for the calcium carbonate directly dissolved by the sodium chloride (0·028 gm. calcium per litre). By deducting the amount of exchangeable calcium present as determined by the first method the amount of exchangeable hydrogen is obtained. The degree of unsaturation was calculated from the formula $100 \times \frac{T-S}{T}$ according to the nomenclature of Hissink (**7**), where S is the amount of exchangeable calcium, and T the total saturation.

Acidity of the soil. This was determined colorimetrically by the use of indicators.

Nitrate. This was determined colorimetrically, using diphenylamine. The following notation was adopted: entirely colourless ($-$), a faint blue ring ($\pm$) denoting a trace, blue ring quite definite ($+$), darker ($++$), deep blue ring ($+++$).

Calcium carbonate. This was determined by measuring the amount of carbon dioxide given off when a known weight of the soil was treated with dilute hydrochloric acid, the Collins calcimeter being used for this purpose.

For soil cultures the sieved soil was mixed with an equal weight of silver sand. The sand was first freed of humus and calcium carbonate in the usual way and later thoroughly washed. The prepared soil was then placed in sterilised earthenware pots and equivalent portions of rhizome (of *Mercurialis perennis*) with a single node planted in them. At the end of the experiment the plants were removed, the soil washed off the roots and the dry weights of the entire plants determined. The exchangeable calcium content and the reaction of the soil were determined both at the beginning and at the end. To avoid the competition factor only one plant was grown in each pot.

PRELIMINARY COMPARISONS OF SOILS.

(1) *Quercetum sessiliflorae on Ludlow beds.*

At the outset of the present investigation observations were made on the soils of the Ludlow beds (Upper Silurian) from the Quercetum sessiliflorae of the Whitecliffe area, Ludlow, Herefordshire. Samples analysed were from a

Vaccinietum myrtilli occupying the summit of the ridge, from a zone of Luzuletum maximae half-way down the slope, and from a *Mercurialis perennis* "flush" community near the bottom of the slope. In no case was there any trace of calcium carbonate in any of the soils. Determinations of the exchangeable calcium contents of the soils from the three zones showed a very interesting state of affairs.

Exchangeable calcium in milligram equivalents.

	0–2 in.	2–6 in.	6–12 in.
Vaccinietum	4·6	0·7	0·7
Luzuletum	10·9	1·5	0·6
Mercurialietum	36·9	37·3	—

Thus it is seen that *Vaccinium myrtillus*, which is markedly calcifuge, is here growing in a soil not only devoid of calcium carbonate but also very poor in exchangeable calcium, especially in the lower layers: *Luzula maxima*, a less marked calcifuge, occupies soil showing a slight increase of exchangeable calcium; while *Mercurialis perennis*, a definite calcicole, inhabits soil which is rich in exchangeable calcium. Thus the question arises: may not the exchangeable calcium itself determine the calcicolous habit? It is not difficult to see that exchangeable calcium may well be more important for a calcicole than calcium carbonate, either by serving as a source of calcium for the plant or by modifying the course of the soil reaction.

(2) *Quercetum sessiliflorae of Bricket Wood (Herts) on non-calcareous Boulder Clay.*

Here a striking correlation between exchangeable calcium and the nature of the plant covering is shown.

A transect was made from the crest of a slope to the bottom, and soil samples taken from the crest, the midslope, and the base. The number of individual plants or separate shoots of the vascular plants present on the area of the soil sample (36 sq. in. = 2·3 sq. dm.) are given below from the three points on the transect (heavy type) as well as from three other points on the crest and two others at the base (ordinary type).

	Crest				Mid-slope	Base		
Pteridium aquilinum	**3**	5	ab.	ab.	—	—	—	—
Luzula pilosa	**rare**	1	—	—	—	—	—	—
Potentilla sterilis	**1**	1	—	—	—	—	—	—
Holcus mollis	—	—	—	f.	—	—	—	—
Oxalis acetosella	—	—	—	—	**1**	—	—	—
Teucrium scorodonia	—	—	—	—	**1**	—	—	—
Fragaria vesca	—	—	—	—	**1**	—	—	—
Ajuga reptans	—	—	—	—	**1**	**1**	—	—
Nepeta glechoma	—	—	—	—	**1**	**1**	1	—
Galeobdolon luteum	—	—	—	—	—	**3**	—	—
Mercurialis perennis	—	—	—	—	—	**14**	6	14
Arum maculatum	—	—	—	—	—	—	3	—
Ficaria verna	—	—	—	—	—	—	—	1

The results of soil analysis of the corresponding areas were as follows. The figures of exchangeable calcium are in milligram equivalents.

	in.	Crest				Mid-slope	Base		
Exchangeable Ca	0–2	**5·9**	3·8	1·9	1·3	**12·6**	**12·8**	14·7	24·2
	2–6	**3·9**	2·9	0·8	0·8	**8·3**	**9·1**	11·5	19·3
$CaCO_3$	0–2	**Nil**	Nil	Nil	Nil	**Nil**	**Nil**	Nil	Nil
	2–6	**Nil**	Nil	Nil	Nil	**Nil**	**Nil**	Nil	Nil
*p*H	0–2	**6·2**	6·0	5·7	5·5	**6·2**	**6·2**	6·4	**6·4**
	2–6	**6·2**	6·0	5·8	5·6	**6·2**	**6·2**	6·4	**6·4**
Nitrates	0–2	**(−)**	(−)	(+)	(±)	**(−)**	**(−)**	(+)	(+)
	2–6	**(−)**	(−)	(±)	(−)	**(−)**	**(−)**	(+)	(+)

Thus there was no detectable calcium carbonate in any of the samples, the *p*H values on the primary transect (heavy type) were the same (6·2), and there was no nitrate reaction in any of the three. At other points on the crest the *p*H was lower and there was some nitrate, while at other points along the bottom of the slope the *p*H was slightly higher and there was also nitrate. But the only consistent difference observed (apart from water content which increased from above downwards) was in exchangeable calcium, which increased markedly down the slope.

The marked disparity between the vegetation of the crest, slope, and base is clear from the table of occurrences of the species, and the correlation with exchangeable calcium is no less obvious. While *Pteridium* grows in a soil rather poor, and is abundant in a soil very poor, in this element, *Mercurialis*, *Arum*, *Ficaria* and *Galeobdolon* grow in soils with much higher calcium content. Where *Pteridium* is abundant and *Holcus mollis* frequent the soil reaction (*p*H 5·5–5·8) is decidedly more acid than those of the soils at the bottom of the slope where the calcicoles predominate (*p*H 6·2–6·4), but the difference is not nearly so marked as that of the exchangeable calcium.

(3) *Fagetum silvaticae at Orpington (Kent) on shallow Clay-with-flints over Chalk.*

Seven areas were compared, three with *Mercurialis*, two with *Pteridium*, one with *Arum*, and one with *Scilla nutans*.

	Exchangeable Ca		*p*H value		Nitrates	
Dominant species	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.
Arum maculatum	14·0	5·0	5·9	5·9	(+ +)	(+)
Mercurialis perennis	11·8	8·9	6·3	6·3	(+)	(±)
„	10·2	6·9	6·3	6·3	(+)	(±)
„	8·6	3·8	5·9	6·0	(+)	(−)
Pteridium aquilinum	6·4	4·9	4·9	5·2	(+)	(−)
„	7·0	0·9	4·6	4·6	(±)	(+)
Scilla nutans	2·7	1·1	4·5	4·6	(−)	(−)

Here too *Mercurialis* grows in a soil with comparatively high exchangeable calcium (8·6–11·8 m.e.), and moderate acidity (*p*H 5·9–6·3) in the surface 2 in., while *Arum*, another calcicole, grows in a soil with comparatively high exchangeable calcium (14·0 m.e.) but of appreciable acidity (*p*H 5·9) in the surface 2 in. In no case was there any detectable calcium carbonate. The case of *Pteridium* is rather interesting. It here grows in a soil of comparatively high acidity (*p*H 4·6–4·9) and of fairly high exchangeable calcium content.

The *Pteridium* found growing here were mostly surface feeding and not deep rooted as usual, and in this surface layer the exchangeable calcium content is 6·4–7·0 M.E. From these results it would appear that the distribution of *Pteridium* is correlated more closely with the acidity than with exchangeable calcium content, to which the species seems to be indifferent, usually growing where this is low, but also where it is sometimes relatively high. At the same time it might appear that the growth of *Mercurialis* also follows the variation in soil acidity rather than that of exchangeable calcium, which by altering the reaction of the soil may make it possible for the *Mercurialis* to grow. But the results of culture experiments show that there is a definite correlation between the growth of *Mercurialis* and the exchangeable calcium content irrespective of reaction.

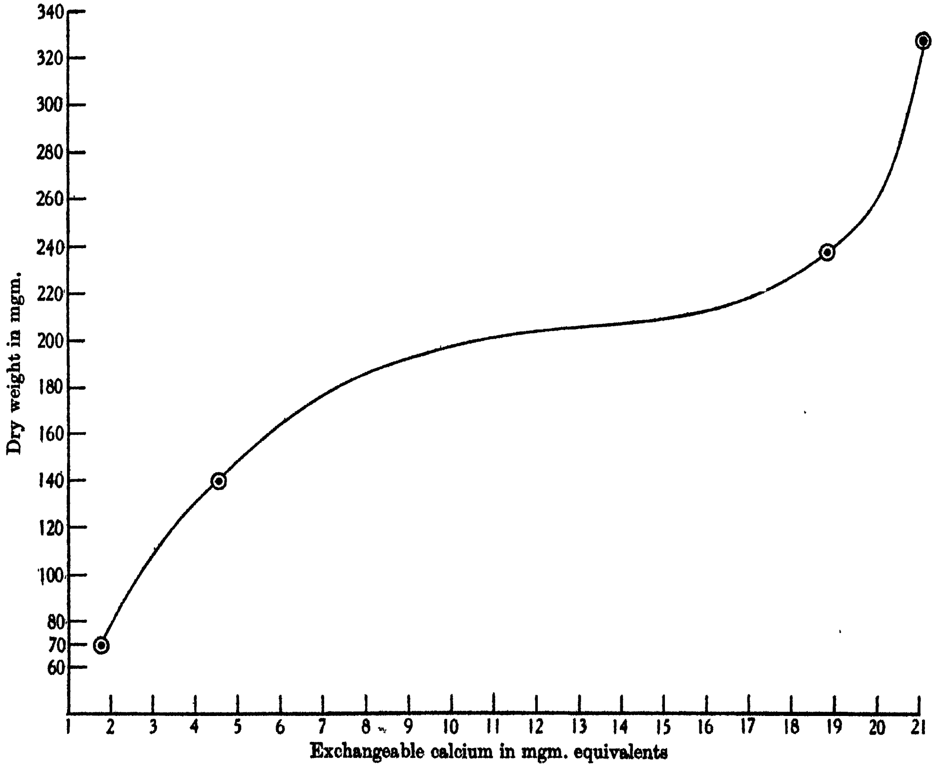

FIG. 1. Growth of *Mercurialis perennis* in relation to exchangeable calcium content of the soil.

Cultivation experiments with Mercurialis *on Bricket Wood soils showing correlation of growth with exchangeable calcium.*

Exchangeable Ca	*p*H value		Nitrates	Dry weight gm.
	At beginning of experiment	At end of experiment		
21·0	6·1	6·9	(±)	0·33
18·8	6·7	6·9	(–)	0·24
4·6	5·9	6·2	(–)	0·14
1·8	5·7	6·2	(±)	0·07

The acidity is not the same in all the soils, but a change in the direction of alkalinity and on the whole towards a greater uniformity has taken place during the course of the experiment. The exchangeable calcium content, on the other hand, remained constant, being the same at the end as at the beginning of the experiment.

The above data show that the acidity of the soil decreased during the course of the experiment, but though the minimum growth of *Mercurialis* was in the soil having the highest acidity there is no gradation in this respect such as is shown by the content of exchangeable calcium both before and after the experiment. The highest acidity at the outset was *p*H 5·7, and at the end 6·2. Such reactions can be accompanied by good growth of *Mercurialis*, as has been found by field observations. Therefore the poor growth in this case cannot be attributable to reaction and one cannot but infer that it is due to the low content of exchangeable calcium.

Individual species.

(1) *Calcifuges.*

Vaccinium myrtillus. This appears to be a strong calcifuge in all respects. The exchangeable calcium content is low, varying from 0·5 to 2 m.e. with an average value of 0·7. The degree of unsaturation varies from 96 to 100 with an average of 98. The acidity ranges from *p*H 4 to 5 with an average of 4·5. Calcium carbonate was absent in all the soils analysed.

Vaccinium myrtillus[1].

(No calcium carbonate occurred in any of the samples.)

	Exchangeable Ca		Ca + H		Unsaturation		*p*H value		Nitrates	
Locality	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.
Ludlow	4·1	1·9	—	—	—	—	4·5	5·0	(–)	(+)
,,	3·0	0·6	13·5	16	78	97	4·1	4·4	(–)	(–)
,,	1·6	0·0	42	10	96	100	4·0	4·3	(–)	(–)
,,	1·4	0·0	30·5	19	98	100	4·0	4·6	(±)	(±)
,,	1·0	0·6	29·5	25	96	98	4·6	4·6	(–)	(–)
,,	—	0·6	—	22·5	—	97	—	4·3	—	(–)
,,	—	0·5	—	25	—	98	—	4·4	—	(–)
,,	—	0·0	—	16·5	—	100	—	4·2	—	(±)
,,	—	0·0	—	12	—	100	—	5·0	—	(–)
	0–6 in.		0–6 in.		0–6 in.		0–6 in.		0–6 in.	
Ludlow	2		31·5		93		4·4		(±)	
Dartmoor	1·5		—		—		4·4		(+ +)	
Ludlow	0·8		27		97		4·3		(–)	
,,	0·0		34		100		4·6		(–)	

Calluna vulgaris is another strong calcifuge. Calcium carbonate is generally absent, perhaps always from the surface soil in which the seedlings develop. The exchangeable calcium content was low, varying from 0·6 to 1·9 m.e. with an average of 1·2. The reaction of the soil varies from *p*H 4·7 to 5·2 with an average of 4·9. The degree of unsaturation varied from 87 to 94 with an average value of 90.

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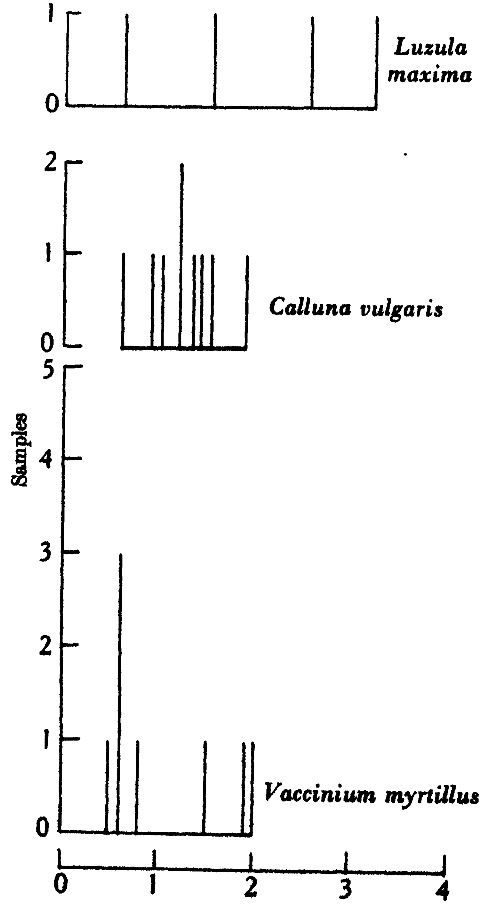
[1] The soil samples in this and the following tables are arranged as far as possible in descending order of exchangeable calcium content.

Calluna vulgaris.

(No calcium carbonate occurred in any of the samples.)

Locality	Exchangeable Ca		Ca + H		Unsaturation		*p*H value		Nitrates	
	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.
Ventnor (I.O.W.)	8·2	1·9	—	—	—	—	4·8	4·9	—	—
,,	3·5	1·3	—	—	—	—	4·9	5·0	—	—
Bricket Wood	2·2	1	11	7·5	81	87	4·7	5·0	(±)	(±)
,,	1·6	1·4	16	12	91	88	4·8	5·0	(–)	(–)
Ventnor (I.O.W.)	1·6	0·6	—	—	—	—	4·8	4·9	—	—
Bricket Wood	1·4	1·2	23·5	10	93	90	5·0	5·2	(–)	(–)
,,	1·4	1·2	24	17·5	93	94	5·0	5·2	(–)	(–)
,,	1·2	0·9	18	15	94	93	4·9	4·9	(–)	(–)
	0–6 in.		0–6 in.		0–6 in.		0–6 in.		0–6 in.	
Dartmoor	1·5		—		—		4·4		(+ +)	



Exchangeable calcium in mgm. equivalents

FIG. 2. Distribution of three calcifuge species in relation to exchangeable calcium in the soil (2–6 in. depth).

Erica cinerea. A high acidity and low exchangeable calcium content was found in two of the three localities examined. In the third the acidity was only moderate and the exchangeable calcium content at the same time much higher. Calcium carbonate was absent from all the samples.

Erica cinerea.

(No calcium carbonate occurred in any of the samples.)

	Exchangeable Ca		*p*H value	
Locality	0–2 in.	2–6 in.	0–2 in.	2–6 in.
Ventnor (I.O.W.)	10·4	7·2	6·2	6·2
,,	3·5	1·3	4·9	5·0
,,	2·2	0·6	4·8	4·8

Ulex europaeus was found growing in soils devoid of calcium carbonate and with an exchangeable calcium content of 1·5 m.e. The acidity of the soil was high.

Ulex europaeus.

(No calcium carbonate occurred in any of the samples.)

	Exchangeable Ca		*p*H value		Nitrates	
Locality	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.
Ventnor (I.O.W.)	4·9	1·5	5·4	5·4	—	—
Hayes	8·9	1·6	4·5	4·8	(-)	(±)

Luzula maxima grows in soils generally devoid of calcium carbonate and containing only small amounts of exchangeable calcium. The latter varied from 0 to 3·2 m.e. with an average value of 1·5 at 2–6 in., higher in the surface soil. The acidity ranged from *p*H 4 to 5 with an average of 4·5 at 2–6 in. The degree of unsaturation varied from 84 to 97 with an average of 91.

Luzula maxima.

(No calcium carbonate occurred in any of the samples.)

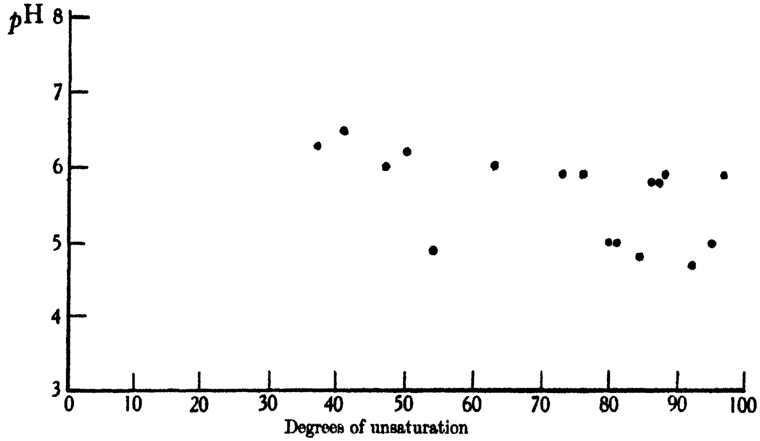
	Exchangeable Ca		Ca + H		Unsaturation		*p*H value		Nitrates	
Locality	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.
Ludlow	5·6	3·2	—	—	—	—	4·0	4·0	(-)	(-)
,,	—	2·5	—	12·5	—	84	—	5·0	(-)	(-)
,,	10·9	1·5	18·5	12·5	40	91	4·6	4·5	(-)	(-)
,,	—	0·6	—	17	—	97	—	4·4	—	(-)
,,	0·6	0·0	—	—	—	—	4·8	4·8	(-)	(±)

Scilla nutans appears to grow in soils poor in calcium carbonate and containing variable but on the whole small amounts of exchangeable calcium. In four varied stations in the same area the exchangeable calcium at 2–6 in. ranged from 0·8 to 5·7. The acidity ranged from 4·5 to 6·0.

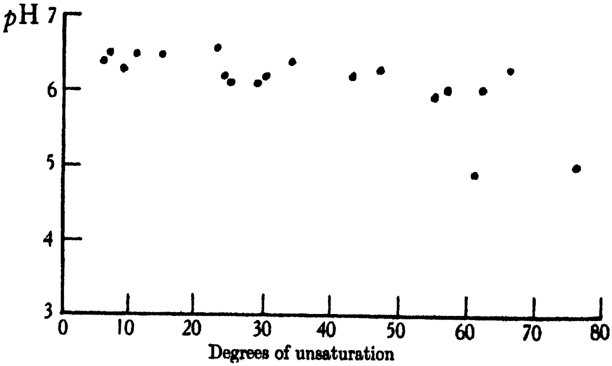
Scilla nutans.

(No calcium carbonate occurred in any of the samples.)

	Exchangeable Ca		*p*H value		Nitrates	
Locality	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.
Bricket Wood	6·2	5·7	4·5	4·5	—	—
,,	—	1·9	—	5·7	—	(-)
,,	2·7	1·1	4·5	4·6	(-)	(-)
,,	1·8	0·8	6·0	6·0	(±)	(-)



Pteridium aquilinum (2–6 in. depth) (and see table on p. 541).



Mercurialis perennis (0–2 in. depth) (and see table on p. 544).

FIG. 3. Distribution of *Pteridium* and *Mercurialis* in relation to *p*H and degrees of unsaturation of soil.

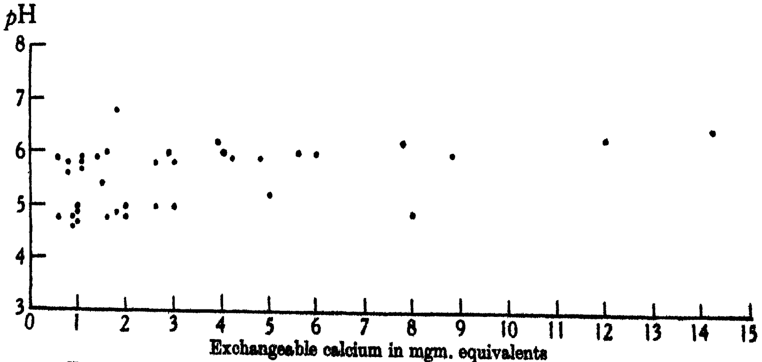


FIG. 4. Distribution of *Pteridium aquilinum* in relation to *p*H and exchangeable calcium in the soil at a depth of 2–6 in.

Pteridium aquilinum usually grows in soils devoid of calcium carbonate and with an exchangeable calcium content generally low. The exchangeable calcium content varied from 0·6 to 14·2 M.E. with an average value of 4·0. Where bracken was found alone the exchangeable calcium varied from 0·6 to 12·9 M.E. with an average of 2·6. Where it was found in association with *Mercurialis* the exchangeable calcium varied from 1·5 to 14·2 M.E. with an average of 5·4. The acidity of the soil varied from *p*H 4·6 to 6·2, with an average of 5·2 in soils where *Pteridium* grew alone, while it ranged from *p*H 4·8 to 6·8 with an average of 5·9 in soils where *Pteridium* and *Mercurialis* were found in association.

Pteridium aquilinum.

(No calcium carbonate occurred in any of the samples.)

	Exchangeable Ca		Ca + H		Unsaturation		*p*H value		Nitrates	
Locality	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.
Bricket Wood	—	14·2	—	24	—	41	—	6·5	—	(±)
,,	—	12·0	—	19	—	37	—	6·3	—	—
,,	—	8·8	—	17	—	47	—	6·0	—	(±)
,,	9·8	8·0	12·5	19·5	51	54	5·0	4·9	(−)	(−)
,,	—	7·8	—	16	—	50	—	6·2	—	—
,,	10·0	6·0	22·5	16	55·5	63	6·0	6·0	—	—
,,	—	5·6	—	—	—	—	—	6·0	—	(−)
,,	—	5·6	—	—	—	—	—	6·0	—	(±)
Orpington	6·4	5·0	—	—	—	—	4·9	5·2	(±)	(±)
Bricket Wood	4·6	4·8	17·5	18·5	74	73	5·8	5·9	(±)	(±)
,,	11·7	4·2	22	17	47	76	6·0	5·9	(±)	(±)
,,	—	4·0	—	—	—	—	—	6·0	—	(−)
,,	—	4·0	—	—	—	—	—	6·0	—	(±)
,,	5·9	3·9	—	—	—	—	6·2	6·2	(−)	(−)
,,	4·8	3·0	18·5	21	73	86	5·8	5·8	(±)	(±)
,,	8·4	3·0	21·5	16	61	81	5·0	5·0	(−)	(±)
,,	3·9	2·9	—	—	—	—	6·0	6·0	(−)	(−)
,,	3·8	2·6	20	19	80	87	5·9	5·8	—	—
,,	8·2	2·6	15	12·5	46	80	5·0	5·0	(−)	(−)
,,	—	2·0	—	—	—	—	—	5·0	—	(±)
,,	—	2·0	—	—	—	—	—	4·8	—	(±)
,,	4·0	1·8	20	17·5	80	88	6·2	5·9	—	—
,,	—	1·8	—	—	—	—	—	6·8	—	(±)
Hayes	9·9	1·6	—	—	—	—	4·5	4·8	(−)	(±)
Bricket Wood	—	1·6	—	—	—	—	—	6·0	—	(−)
,,	—	1·6	—	—	—	—	—	4·8	—	(±)
Ventnor	5·0	1·5	—	—	—	—	5·4	5·4	—	—
Bricket Wood	—	1·4	—	—	—	—	—	5·9	—	(−)
Orpington	—	1·1	—	—	—	—	—	5·9	—	(−)
,,	—	1·1	—	—	—	—	—	5·8	—	(−)
Bricket Wood	—	1·1	—	—	—	—	—	5·7	—	(±)
Ventnor	2·0	1·0	—	—	—	—	4·9	4·9	—	—
Bricket Wood	2·4	1·0	15	13	83	92	4·8	4·7	(±)	(±)
,,	4·6	1·0	35	20·5	87	95	4·8	5·0	(±)	(±)
Hayes	5·4	0·9	—	—	—	—	4·6	4·8	(±)	(±)
Orpington	7·0	0·9	—	—	—	—	4·6	4·6	(±)	(−)
Bricket Wood	1·9	0·8	—	—	—	—	5·6	5·8	(±)	(±)
,,	1·4	0·8	—	—	—	—	5·6	5·6	(±)	(−)
,,	2·9	0·6	—	—	—	—	4·7	4·8	(±)	(−)
,,	3·9	0·6	25·5	17	84	84	4·8	4·8	(±)	(±)
,,	2·4	0·6	25	18	90	97	5·9	5·9	(±)	(±)

(2) *Calcicoles.*

Arum maculatum. This grows in soils rich in exchangeable calcium even when calcium carbonate is absent. The observed range of exchangeable calcium was from 4·5 to 19·9 M.E. with an average value of 12·3. The reaction of the soil ranged from *p*H 5·9 to 7·0 with an average value of 6·4. The degree of unsaturation also has rather a narrow range, varying from 7 to 25 at 0–2 in. with an average of 16.

Arum maculatum.

	Exchangeable Ca		Ca + H		Unsaturation		*p*H value		Nitrates		$CaCO_3$	
Locality	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.
Hayes	19·9	17·2	—	—	—	—	7·0	7·0	(+ +)	(+)	0·486	1·017
"	18·6	17·6	—	—	—	—	6·8	6·8	(+)	(+ +)	0·216	0·243
Bricket Wood	14·6	11·0	16·5	15	12	21	6·5	5·9	(±)	(±)	Nil	Nil
Hayes	14·2	12·3	—	—	—	—	6·8	6·8	(+)	(±)	0·198	0·324
Orpington	14·0	5·0	—	—	—	—	5·9	5·9	(+)	(±)	Nil	Nil
Bricket Wood	13·4	10·8	14·5	12	7	8	6·5	6·5	(±)	(±)	"	"
"	12·0	10·4	16	13	25	19	6·5	6·4	(±)	(±)	"	"
"	11·4	11·4	13	12·5	11	8	6·5	6·5	(±)	(±)	"	"
"	11·0	12·6	13	15·5	15	19	6·3	6·4	(±)	(±)	"	"
"	9·6	9·6	12·5	13·5	24	30	6·4	6·2	(+)	(±)	"	"
"	9·0	8·4	—	—	—	—	6·1	6·0	(±)	(±)	"	"
"	7·6	4·6	9·0	8·5	16	47	6·2	6·1	(±)	(±)	"	"
"	5·0	4·5	6·0	8·0	17	43	6·1	6·1	(±)	(±)	"	"

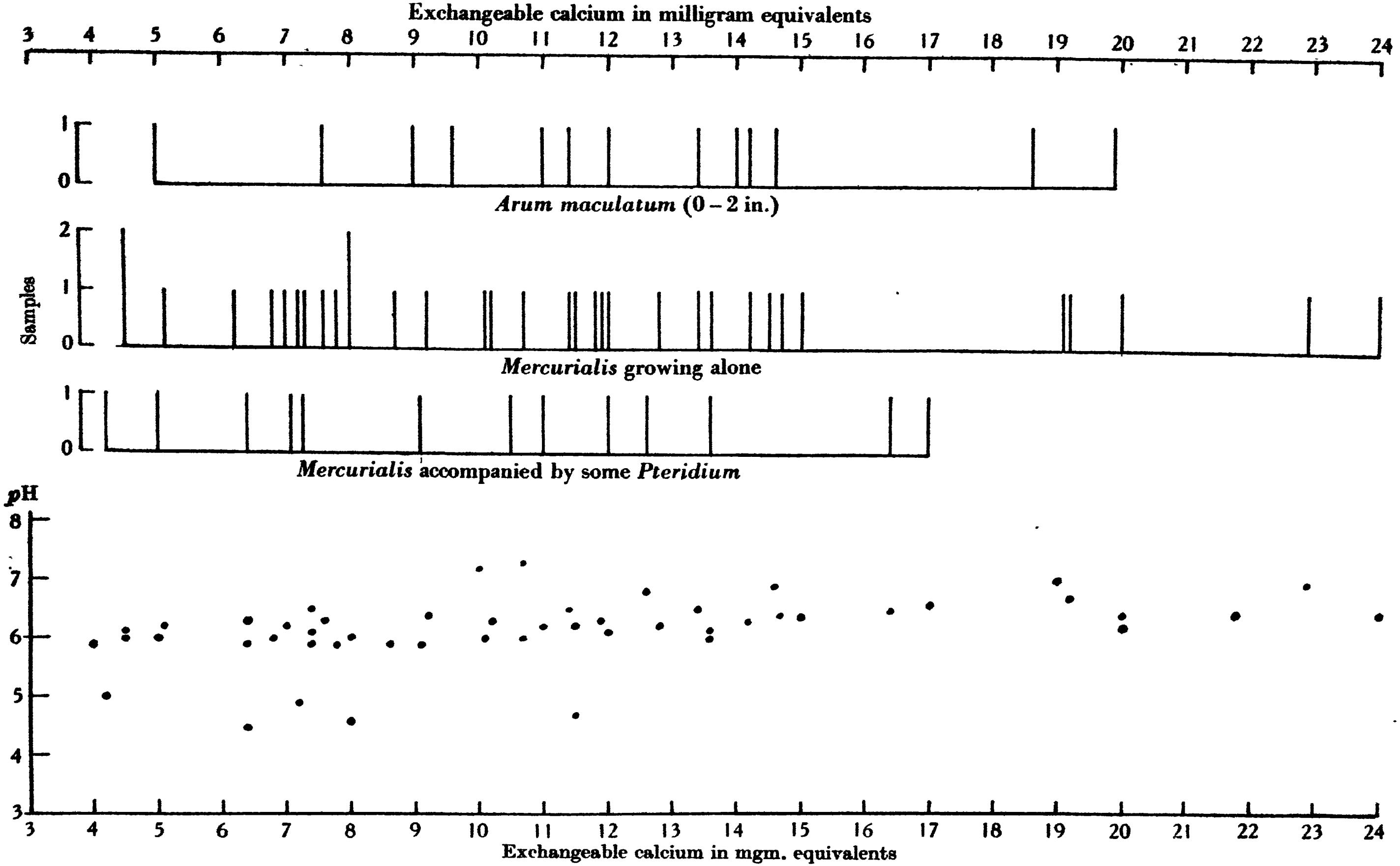
Hordeum silvaticum, a species sometimes considered as characteristic of beechwoods on chalk, was found by Dr Butcher growing in soil which proved to be devoid of calcium carbonate but contained a moderate amount of exchangeable calcium. Samples taken from two loci, one at the bottom of a slope and the other higher up, showed exchangeable calcium of 19·6 and 12·6 M.E. respectively. The reaction of the soil was *p*H 6·3 and 6·0 and nitrates (+) in both cases. The degree of unsaturation showed a big difference, 7 and 50 respectively. Here too the distribution of the species appears to be correlated with content of exchangeable calcium.

Hordeum silvaticum.

(No calcium carbonate occurred in either of the samples.)

	Exchangeable Ca 0–6 in.	Ca + H 0–6 in.	Unsaturation 0–6 in.	*p*H value 0–6 in.	Nitrates 0–6 in.
Tees Valley	12·6	25	50	6·0	(+)
Barnard Castle	19·6	21	7	6·3	(+)

Mercurialis perennis. This generally grows in soils containing calcium carbonate, rich in exchangeable calcium and having a low acidity, but these factors are subject to wide fluctuations. It has been found to grow in soils with, and in soils without, calcium carbonate, and an exchangeable calcium content varying from 4·2 to 24 M.E. (average value 11). Where *Mercurialis* was found alone this varied from 4·5 to 24; where in association with *Pteridium* from 4·2 to 17. The acidity of the soil ranged from *p*H 4·5 to 7·3 with an



Mercurialis perennis (0–2 in. depth).

FIG. 5. Distribution of calcicole species in relation to exchangeable calcium in the soil and to *p*H.

average of 6·0. Where *Mercurialis* grew alone the *p*H ranged from 4·5 to 7·3; where *Mercurialis* was found in association with *Pteridium* it ranged from *p*H 4·9 to 6·8 with an average of 5·9 (see Fig. 5). The degree of unsaturation ranged from 6 to 66 with an average of 33 where *Mercurialis* was alone, and from 15 to 78 with an average of 44 where *Mercurialis* was in association with *Pteridium*. The species thus has a considerable range of tolerance towards all the factors considered, provided probably that all the factors are not working unfavourably at the same time.

Mercurialis perennis.

	Exchangeable Ca		Ca + H		Unsaturation		*p*H value		Nitrates		$CaCO_3$	
Locality	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in
Bricket Wood	24	19·3	—	—	—	—	6·4	6·4	(±)	(±)	Nil	Nil
"	22·9	—	—	—	—	—	6·9	—	(+)	—	"	—
"	21·8	—	—	—	—	—	6·4	—	(±)	—	"	—
"	20·0	15·0	30·5	25·5	34	40	6·4	6·2	(±)	(±)	"	Nil
"	20·0	13·4	26·5	18·5	24	27	6·2	6·1	(±)	(±)	"	"
"	19·2	—	—	—	—	—	6·7	—	(±)	—	"	—
"	19·0	—	—	—	—	—	7·0	—	(±)	—	"	—
"	17·0	—	22	—	23	—	6·6	—	(±)	—	"	—
"	16·4	—	19·5	—	15	—	6·5	—	(±)	—	"	—
"	15·0	14·8	18	16·5	6	9	6·4	6·4	(+)	(+)	"	Nil
"	14·7	11·5	—	—	—	—	6·4	6·4	(+)	(+)	"	"
"	14·6	—	—	—	—	—	6·9	—	(−)	—	"	—
"	14·2	14·2	15·5	14·5	9·5	4	6·3	6·3	(±)	(±)	"	Nil
"	13·6	—	—	—	—	—	6·0	—	(−)	—	"	—
"	13·6	11·4	18	17	25	32	6·1	6·1	(±)	(±)	"	Nil
"	13·4	10·8	14·5	12	7	8	6·5	6·5	(±)	(±)	"	"
"	12·8	9·1	—	—	—	—	6·2	6·2	(−)	(−)	"	"
"	12·6	—	—	—	—	—	6·8	—	(+)	—	"	—
"	12·0	8·2	17	13	20	38	6·1	6·3	(±)	(±)	"	Nil
Orpington	11·9	8·9	—	—	—	—	6·3	6·3	(+)	(±)	"	"
Berkhamsted	11·5	9·9	—	—	—	—	4·7	4·7	(+)	(+)	"	"
Bricket Wood	11·5	—	—	—	—	—	6·2	—	(±)	—	"	—
"	11·4	11·4	13	12·5	11	8	6·5	6·5	(±)	(±)	"	Nil
"	11·0	—	19·5	—	43	—	6·2	—	—	—	"	—
Ventnor	10·7	6·9	—	—	—	—	7·3	7·3	(±)	(±)	34·8	28·8
Bricket Wood	10·7	—	—	—	—	—	6·0	—	(−)	—	Nil	—
Orpington	10·2	6·9	—	—	—	—	6·3	6·3	(+)	(±)	"	Nil
Bricket Wood	10·1	—	—	—	—	—	6·0	—	(−)	—	"	—
Ventnor	10·0	18·3	—	—	—	—	7·2	7·2	—	—	23·5	25
Bricket Wood	9·2	—	—	—	—	—	6·4	—	(−)	—	Nil	—
"	9·1	—	—	—	—	—	5·9	—	(+)	—	"	—
Orpington	8·6	3·9	—	—	—	—	5·9	6·0	(+)	(−)	"	Nil
Wyre Forest (Worc.)	8·0	—	—	—	—	—	4·6	—	(−)	—	"	—
Bricket Wood	8·0	6·0	19	15·5	57	61	6·0	6·0	—	—	"	Nil
"	7·8	5·0	18	16	55	68	5·9	6·0	(±)	(±)	"	"
"	7·6	4	22·5	20·5	66	80	6·3	6·3	(±)	(±)	"	"
"	7·4	—	—	—	—	—	6·5	—	(−)	—	"	—
"	7·4	—	—	—	—	—	6·1	—	(±)	—	"	—
Orpington	7·2	—	—	—	—	—	5·9	—	(−)	—	"	—
Bricket Wood	7·1	—	18	—	61	—	4·9	—	(−)	—	"	—
"	7·0	6·4	10	13	30	50	6·2	5·9	(±)	(±)	"	Nil
"	6·8	3·8	18·5	16·5	62	75	6·0	6·1	—	—	"	"
"	6·4	—	—	—	—	—	5·9	—	(−)	—	"	—
Ludlow	6·4	—	—	—	—	—	4·5	—	(−)	—	"	—
Bricket Wood	6·2	3·0	11·5	11·5	47	74	6·3	5·9	(±)	(±)	"	Nil
"	5·1	—	—	—	—	—	6·2	—	(±)	—	"	—
"	5·0	—	—	—	—	—	6·0	—	(−)	—	"	—
Orpington	4·5	—	—	—	—	—	6·0	—	(−)	—	"	—
Bricket Wood	4·5	—	—	—	—	—	6·1	—	(+)	—	"	—
"	4·2	—	18·5	—	76	—	5·0	—	(±)	—	"	—
"	4·0	—	—	—	—	—	5·9	—	(−)	—	"	—

Fagus silvatica, Daphne laureola and **Allium ursinum** are species that appear to grow in soils rich in exchangeable calcium. This, rather than the calcium carbonate content, appears to influence their distribution, as may be seen from the figures given below.

		Exchangeable Ca 0–6 in.	Ca + H 0–6 in.	Unsaturation 0–6 in.	*p*H value 0–6 in.	Nitrates 0–6 in.	$CaCO_3$ 0–6 in.
Allium ursinum:	Ventnor	17·9	—	—	6·0	—	Nil
Daphne laureola:	Bishops Wood	12·0	15·5	16	6·6	(±)	1·26
Fagus sylvatica:	Bucks	49·4	—	—	7·0	(+ + +)	35
	Sussex	44	—	—	7·0	(−)	0·5

Nitrifying bacteria. As a community nitrifying bacteria seem to be somewhat indifferent to all the factors considered—calcium carbonate, exchangeable calcium and soil reaction. They were found to function with great vigour only in a few instances, and in almost all cases the soils contained appreciable amounts of calcium carbonate. The few instances in which there was anything more than a (+ +) reaction for nitrates were in soils containing calcium carbonate, as in a beechwood and in some *Arum* communities. Further, of two beechwoods examined one had 35 per cent. calcium carbonate and the other only 0·5 per cent., while in both the acidity was the same (*p*H 7·0) and exchangeable calcium nearly the same (49·4 and 44 M.E.). The former, however, showed (+ + +) nitrates and the latter (−).

From these examples the nitrifying bacteria would appear to follow the distribution of calcium carbonate. Further, hardly any of the Bricket Wood samples showed any detectable calcium carbonate and hardly any of the soils showed nitrates more than (+) even after a long period of dry weather. And there is a large majority of cases in which nitrifying bacteria were found to function with reduced vigour, as indicated by (+) or (±) nitrates in soils which contained no trace of calcium carbonate, little exchangeable calcium and showed a high acidity.

Nevertheless, in one case there was (+ +) nitrates in a *Vaccinium* community where the soil contained no calcium carbonate, only 1·5 M.E. exchangeable calcium and had an acidity as high as *p*H 4·4. Further, in a sample of soil where *Daphne laureola* was growing there was only a trace of nitrate shown in spite of the fact that calcium carbonate was present (1·26 per cent.), exchangeable calcium content rather high (12 M.E.) and acidity low (*p*H 6·6). A similar state of affairs existed in soil bearing *Arum maculatum*. There were 0·19 and 0·32 per cent. calcium carbonate in the two layers, 14·2 and 12·3 M.E. of exchangeable calcium, and acidities of *p*H 6·8 and 6·8 respectively. Thus, while nitrifying bacteria seem normally to flourish in soils with calcium carbonate and appreciable exchangeable calcium combined with a low soil acidity, they have also been found to function with reduced vigour in soils which are quite acid and with no calcium carbonate and little exchangeable calcium.

Nitrates.

Locality	Nitrates		Exchangeable Ca		Ca + H		Unsaturation		pH value		$CaCO_3$	
	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.
Beechwood (Bucks)	(+ + +)		49·4		—		—		7·0		35	
Beechwood (Sussex)	(–)		44·0		—		—		7·0		0·5	
Hayes	(+ +)	(+)	19·9	17·2	—	—	—	—	7·0	7·0	0·48	1·01
"	(+)	(+ +)	18·6	17·6	—	—	—	—	6·8	6·8	0·21	0·24
Dartmoor	(+ +)		1·5		—		—		4·4		Nil	
Bricket Wood	(+)	(+)	6·2	5·7	—	—	—	—	4·5	4·5	Nil	Nil
Bishops Wood	(±)		12		15·5		16		6·6		1·26	
Hayes	(+)	(±)	14·2	12·3	—	—	—	—	6·8	6·8	0·19	0·32
Bricket Wood	(+)	(±)	9·6	9·6	12·5	13·5	24	30	6·4	6·2	Nil	Nil
Orpington	(±)	(±)	14·0	5·0	—	—	—	—	5·9	5·9	"	"
Bricket Wood	(+)	(±)	24·0	19·3	—	—	—	—	6·4	6·4	"	"
"	(+)	(±)	20·0	13·4	26·5	18·5	24	27	6·2	6·1	"	"
Orpington	(+)	(±)	11·9	8·9	—	—	—	—	6·3	6·3	"	"
Berkhamsted	(+)	(+)	11·5	9·9	—	—	—	—	4·7	4·7	"	"
Bricket Wood	(±)	(+)	7·0	6·4	10·0	13·0	30	50	6·2	5·9	"	"
Orpington	(±)	(+)	6·4	5·0	—	—	—	—	4·9	5·0	"	"
Bricket Wood	(±)	(±)	4·6	4·8	17·5	18·5	74	73	5·8	5·9	"	"
Hayes	(–)	(+)	9·9	1·6	—	—	—	—	4·5	4·8	"	"
Bricket Wood	(±)	(±)	1·9	0·8	—	—	—	—	5·6	5·8	"	"
Ludlow	(–)	(±)	0·6	0·0	—	—	—	—	4·8	4·8	"	"
Bricket Wood	(±)	(±)	2·2	1·0	11	7·5	81	87	4·7	5·0	"	"
Ludlow	(±)	(±)	1·4	0·0	30·5	19·0	98	100	4·0	4·6	"	"

DISCUSSION.

The so-called calcicolous plants normally grow in soils containing calcium carbonate or exchangeable calcium, and soils which are alkaline, neutral or of relatively low acidity. In a number of cases it would appear difficult to say whether their distribution in reality follows the soil reaction, which is automatically rendered less acid by the presence of quantities of calcium. But culture experiments would seem to show that the distribution of calcicoles, especially *Mercurialis perennis*, can be correlated with soil content of exchangeable calcium. Further, there are a few cases where calcicolous plants have been found to grow in soils of appreciable acidity but at the same time containing large amounts of exchangeable calcium. The following analyses of soils bearing *Mercurialis perennis*, one from Berkhamsted, one from Wyre Forest and the last from the Whitecliffe area, Ludlow, are all cases in point. Calcium carbonate was absent from all the soils.

	Exchangeable Ca		pH value		Nitrates	
	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.
Berkhamsted	11·5	9·9	4·7	4·7	(+)	(+)
Wyre Forest	8·0	—	4·6	—	(–)	—
Whitecliffe	6·4	—	4·5	—	(–)	—

Here one had healthy growth of *Mercurialis* in soils devoid of calcium carbonate and with distinctly high acidity, but containing moderate quantities of exchangeable calcium. Hence, of the factors considered, growth in these soils can only be correlated with exchangeable calcium. Moreover, it has been shown by Robinson and Williams (**13**) that "unsaturation, i.e. the presence of free alumino-silicic and humic acids, is not inconsistent with fertility and that many soils in this condition do not respond to liming. An examination of such soils by the Hissink method reveals the presence of considerable proportions of exchangeable calcium. Certain soils, on the other hand, which respond to lime are shown to contain only small proportions of exchangeable calcium." The above observation may clearly be the explanation of the growth of *Mercurialis* in the acid soils cited above.

Calcifuges, on the other hand, normally grow in soils devoid of calcium carbonate and containing little exchangeable calcium. The acidity of the soil is generally high. In these cases it is difficult to say whether the plant is really calcifuge in the literal sense of the word or whether it is the reaction of the soil that is of importance. Occasionally *Pteridium* has been found growing in soils relatively rich in exchangeable calcium, but with an appreciable acidity. In one spot on the top of the heath at Bricket Wood, where *Pteridium* is almost exclusively dominant, it was observed that some refuse had recently been dumped and in that spot very healthy and abundant *Mercurialis* was growing. The mercury was obviously a late arrival and bracken also was growing quite well. Analysis of this soil showed:

Exchangeable Ca		Ca + H		Unsaturation		*p*H value		Nitrates		$CaCO_3$	
0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.	0–2 in.	2–6 in.
17	8·8	22	17	23	47	6·0	6·0	(±)	(±)	Trace	Trace

The exchangeable calcium content is here higher than usual for this area, especially in the subsurface layer (2–6 in.). Such a high value as 8·8 M.E. for this layer is very rare for the top of the heath. The degree of "unsaturation" too is a good deal less than in the typical heath soil. The arrival of the *Mercurialis* in this patch of soil, where it has not been observed before, has been rendered possible by the change in the soil resulting from the dumping of rubbish and the consequent increase in exchangeable calcium. The growth of *Pteridium* here is probably a case parallel to that of *Calluna* observed by Prof. Salisbury where the seedling stage is calcifuge while the mature plant can tolerate quantities of calcium. Or it may be, as Lundegårdh (**10**, p. 219) remarks: "the plants classed as calciphobes do not avoid the calcium ion as such, but cannot endure the alkaline reaction which accompanies it, or the change in permeability which the calcium ion produces."

The association of *Mercurialis* and *Pteridium* in the same spot is probably partly due to the degree of tolerance shown by *Pteridium* towards exchangeable calcium. Generally the reaction of the soil is about the same in both surface and subsurface soil layers where the *Mercurialis* and the *Pteridium* are respectively rooted, while the content of exchangeable calcium shows a difference, being higher in the surface than in the subsurface layer. Thus the root systems of the two species are in the two layers where the conditions are fairly close to normal for each species. On the other hand, the two are often found together on soils whose acidity is higher than is normal for *Mercurialis* and with an exchangeable calcium content higher than is normal for *Pteridium*. Their existence together in such cases is most probably due to the latitude in their reaction to exchangeable calcium content and acidity.

Other calcicoles, such as *Arum*, and other calcifuges, such as *Calluna* or *Vaccinium*, have a narrow range both in respect to exchangeable calcium and acidity. In the case of *Arum* the former is apparently high and the latter low, while the opposite holds for *Calluna* and *Vaccinium*. It is possibly a consequence of this relation that one so rarely finds most calcicoles and calcifuges in company, whereas it is a common sight to see *Mercurialis* and *Pteridium* growing together.

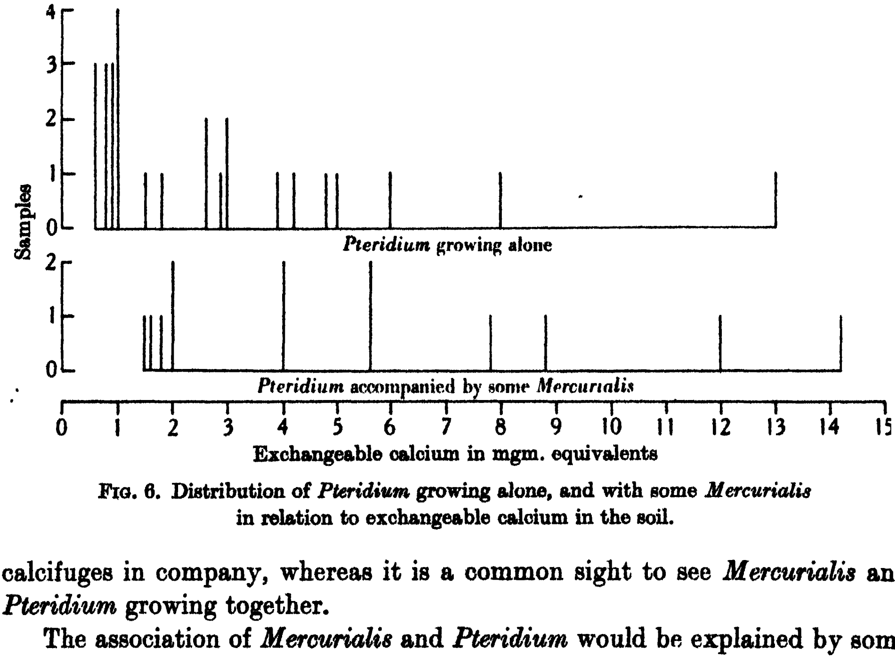


FIG. 6. Distribution of *Pteridium* growing alone, and with some *Mercurialis* in relation to exchangeable calcium in the soil.

The association of *Mercurialis* and *Pteridium* would be explained by some as due to the existence of better water relations which enable either species to tolerate the somewhat abnormal habitat conditions. Thus Lundegårdh writes: "there were perfectly clear cases of well-recognised chalk plants, such as *Pulsatilla* and *Hippocrepis comosa*, growing on siliceous soil almost free from chalk; but they were only to be found where the physical constitution of the siliceous soil, its temperature and water content were similar to those of chalk (Lundegårdh (**10**)). And Salisbury: "In woods on acid soils the calcicolous *Mercurialis perennis* occurs either in dry areas with a high calcium content (or low acidity) or in damp areas where the lime requirement is high considered in terms of unit of weight of dry soil (total acidity) but is apparently ameliorated as a consequence of the high water content" (Salisbury (**14**)).

Of course the calcium content here referred to is probably the carbonate, and therefore the "damp areas" mentioned may well have contained a high content of exchangeable calcium. Rather extensive observations carried out in the field (at Bricket Wood) led the writer to the conclusion that the water content of the soil is not responsible for the association of *Pteridium* and *Mercurialis*. Thus the following percentages of water were found below *Pteridium* and *Mercurialis*:

Pteridium	26·1	Mercurialis	26·5
Pteridium	47·4	Mercurialis	39·9
Pteridium and Mercurialis	34·4		
Pteridium and Mercurialis	25·1		

These figures from a few selected localities suggest that there is a certain indifference to water content on the part of both species.

It is well known to British ecologists that the beech, so characteristic of the chalk downs, also occurs in natural woods on soils destitute of calcium carbonate, such as the Wealden sands, the Lower Greensand, and the Eocene sands on the edge of the London basin, while it forms extensive woods on the non-calcareous clay-with-flints of the Chiltern plateau. It is therefore possible that some of the normally calcicolous species which occur also on soils deficient in calcium carbonate are nevertheless adequately supplied with exchangeable calcium. It is the exchangeable calcium and not the calcium carbonate that is directly available to the growing plant. "In the absence of exchangeable calcium the plant does not develop unless a calcium salt is added to serve as a source of calcium for the plant. That portion of calcium which is not exchangeable cannot be assimilated in sufficient quantities required for growth" (Gedroiz (6)).

It is possible that *Mercurialis* can sometimes grow under conditions in which there is little calcium because what there is occurs in a readily available condition. "Hissink showed that a part of the replaceable calcium can be easily removed from soils by extraction with carbonated water. He holds that the soil when so treated becomes unsaturated with bases, that is, hydrogen ions of the carbonated water displace the bases from the soil" (Kelley and Brown (9)). Also "when a plant is grown in such a soil more or less calcium will be absorbed by the plant. This is made possible through the intervention of hydrogen ions. The soil moisture always contains more or less carbonic and other acids formed by microbiological processes. The hydrogen ions of these acids react in ion exchange with the replaceable calcium, bringing the calcium into solution and thus making it available" (Kelley (8)). Thus it is possible that in these cases conditions arise which make the little exchangeable calcium more readily available. What these conditions are it is difficult to say.

Further observations carried out at Bricket Wood in the early spring of 1932 showed the extreme commonness of the association of *Pteridium* and *Mercurialis*. Except at the top of the heath where the acidity is high and the calcium content low it was difficult to find localities where *Pteridium* alone grew. It is quite possible that, just at this time of the year, leaves which were deposited the autumn before may have delivered their calcium content to the surface layers of the soil, enriching it in calcium and making it favourable for the growth of *Mercurialis*, which is a surface feeder. If this is the case it gives strong support to the view that exchangeable calcium is a determining factor in the growth of *Mercurialis.*

The original theory of the influence of physical rather than chemical conditions on the distribution of calcicolous and calcifugous species was really based on the idea that calcicoles always grew on soils containing calcium carbonate, and where the latter is found in quantity the soil is always light and dry. On the other hand, calcifuges appeared on soils free from calcium carbonate, containing much humus, and thus with a high water-retaining capacity. As a result of general observations in the field and analysis of such soils in respect to calcium carbonate and exchangeable calcium content, it has become evident that calcicoles are not limited to dry well-aerated areas, but that when they occur in soils devoid of calcium carbonate these soils are rich in exchangeable calcium.

The exchangeable calcium content of a soil is really a function of the clay fraction of the soil which is the active agent of the exchange phenomenon. Therefore the greater the exchangeable calcium content or saturation capacity of a soil, the more clayey, and therefore the heavier and moister, the soil tends to be. A consideration of the areas where *Pteridium* and *Mercurialis* are associated leads to the same result. *Pteridium* is deep rooted and *Mercurialis* is a surface feeder. The water-retaining capacity often decreases from the surface downwards owing to the decrease in humus. Thus the calcicole is growing in the moister soil layer while the calcifuge is rooted in the soil layer less retentive of water. But the amount of exchangeable calcium also often decreases from the surface downwards, and it is with this factor that the distribution of the two species is correlated.

As regards the calcifuges, they often grow in soils which are moist, but this is a necessary consequence of the other factors involved. They grow in leached soil entirely devoid of calcium carbonate and containing little exchangeable calcium. In spite of the fact that there is little exchangeable calcium the exchange capacity is high. This means a high clay fraction and thus a heavy and moist soil. Further the acidity is high also, owing both to the presence of humic acids and the unsaturated nature of the clay fraction. This inhibits the activity of soil micro-organisms and there will therefore be an accumulation of humus, which again is a water retainer. On the whole, examination of the exchangeable calcium content of the soil reveals a greater significance of the chemical than of the physical aspect of the soil in relation to plant distribution, though the physical aspect cannot be wholly ignored.

Pearsall (**12**) considers that it is not the reaction of the soil that determines the growth of particular species, but the "basic ratio," Na + K : Ca + Mg, of a soil. Calcium is the ion that is most easily leached, and in soils where calcium is low the basic ratio is correspondingly high, and the resulting type is acid. This view has been rather severely criticised. "One can therefore conclude that for land plants the basic ratio has little, if any, significance, and that the main factor which is responsible for the incidence of species is the reaction of the soil, which is one of the several factors that govern the distribution of plants in the wild state" (Salisbury (**16**)). From the results of the work described in this paper the writer would tend to believe that both views may express some truth. Where the soil is fully leached of calcium carbonate the plants will have to depend for their supply of calcium entirely on the exchangeable bases. As regards the other bases there is always a constant reserve stock available if the exchangeable bases tend to be depleted; but in the absence of calcium carbonate it is not so for calcium. At the same time calcium forms the bulk of the exchangeable bases, while the others are in comparatively small amounts. As the exchangeable bases can be leached by carbonated water, the bases, mainly calcium, will be leached under normal conditions of rainfall, and their places will be taken by hydrogen ions. As calcium ions are replaced by hydrogen ions more readily than the other bases the ratio Na + K : Ca + Mg will gradually tend to rise. Thus the basic ratio has become high and the plant type will tend to be acidophil as Pearsall observed. But of course the acidity too has increased, owing to the increase in hydrogen ions, and as stated by Salisbury the incidence of species may be attributed to the reaction of the soil. There are cases where the soil has little humus and the amount of humic acid is small, while the soil is not very clayey and there is thus little chance of the presence of an acid clay. In such cases a little leaching makes a big difference in the basic ratio without any appreciable change in the soil reaction. A probable case in point is the first set of Bricket Wood soils given at the beginning of this paper (p. 534). In the transect down the slope (figures in heavy type) all three samples show the same reaction but different amounts of exchangeable calcium, and the plant covering is determined, at least in this case, by the amount of exchangeable calcium. In such cases Pearsall's statement would be true, though the writer inclines to believe that it is really the exchangeable calcium and not the basic ratio as a whole that is responsible for the particular type of plant growth. Most calcicoles would react to the exchangeable calcium content more than to anything else provided the acidity is not high. In cases where the soil is of a low saturation capacity leaching would readily make a difference to the plant growth. Such a soil would bear an acidophil type of plant covering, though the soil is not very acid in reaction, simply owing to the lack of calcium.

SUMMARY.

The distribution of calcicole and calcifuge species has generally been associated with the presence and absence respectively of calcium carbonate. Little or no notice has been taken of the occurrence of marked calcicoles like *Arum maculatum* on soils without any detectable trace of calcium carbonate. Data are presented which show that in all such cases the soils contain considerable quantities of exchangeable calcium. *Arum maculatum* is invariably associated with a high content of exchangeable calcium and low acidity. On the other hand, calcifuges like *Vaccinium myrtillus* are associated with a low content of exchangeable calcium combined with moderately high acidity. *Mercurialis perennis*, though common on soils with high exchangeable calcium, is also found on soils with low exchangeable calcium provided the acidity is low. Similarly *Pteridium*, though commonest on soils with low exchangeable calcium, is sometimes found on soils with moderate exchangeable calcium provided the acidity is fairly high. It is probably this latitude in respect of exchangeable calcium and soil acidity that has made possible the association of these two species on soils containing no calcium carbonate.

The nitrifying bacteria, as a community, are not well defined in their reaction to any of the factors considered. They have been found to flourish in soils containing calcium carbonate and consequently of low acidity. But they have also been found to function, though with less vigour, in acid soils where *Vaccinium* and *Calluna* grew.

On the whole the distribution of calcicoles appears to be correlated with content of exchangeable calcium, and the results of culture experiments confirm this view. The calcifuges appear to follow the soil reaction.

In conclusion the writer would like to record his sincere thanks for the ungrudging help given by Prof. E. J. Salisbury and Dr Paul Haas throughout the course of this investigation.

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SUCCESSION, DEVELOPMENT, THE CLIMAX, AND THE COMPLEX ORGANISM: AN ANALYSIS OF CONCEPTS[1]. PART I.

BY JOHN PHILLIPS.

CONTENTS.

PAGE

INTRODUCTION 554

The controversy regarding certain basic concepts 555

Objects of the present contribution 555

SUCCESSION: ESSENTIAL NATURE AND DIRECTION:

The universality of change 556

The nature and causes of change 557

Concepts: Succession is due to:

Any cause, and is either progressive or retrogressive 557

Any cause, and is either progressive or retrogressive; if change be gradual 561

Any cause, and is either progressive or retrogressive; if progressive, due to reactions; if retrogressive, due to causes other than reactions . 561

Any cause, but is progressive only 562

Biotic reactions only, and is always progressive 562

Any cause except biotic reactions 563

Biotic reactions only, and is progressive and retrogressive 563

Convergence and divergence 563

Modifications in succession 565

CONCLUSIONS AND SUGGESTIONS 565

Conclusions 565

Suggestions 567

REFERENCES 570

INTRODUCTION.

CRITICISM, destructive and constructive, acts as an elixir upon the ecologist, forcing him to re-examine the bases of his suppositions and beliefs. During the last five years I have frequently been cross-examined, verbally and by letter, as to certain of my views regarding plant ecology in South and East Africa, as well as upon the tenets of leading workers such as Clements, Tansley, and members of the phyto-sociological schools of Europe. Perhaps an especially remarkable feature of criticism received has been that it has come largely either from those who are neither botanists nor ecologists, or from assistants and students in the course of training for ecological work. I submit, therefore, to professed ecologists, that our concepts may be shrouded in nebulous covering in our literature—due doubtless to our admitted inherent lack of certainty and agreement.

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[1] In which is included a reply to **A. P. G. Michelmore**, This JOURN. **22**, No. 2, pp. 313–17, 1934.

Some of the more provocative observations have come from C. Gillman (1931–2), the well-known East African geomorphologist, in personal communications to which I make reference under a special heading. To certain of these Michelmore (1934) has added, in that he criticises the principle underlying my linking up of certain vegetation communities in successional chains, and concludes that ecologists do not sufficiently recognise the difference between succession due to changes brought about by plants themselves, and succession due to changes not governed by plants; that the first kind of succession rarely occurs between the different stages of natural vegetation—except as the result of "artificial" changes; and that the real climax vegetation of a region is not a single type but a whole series of types. While it is my intention to deal specifically—under the same heading dealing with Gillman's observations—with Michelmore's criticisms, I propose to refer to certain of his views in the analyses of concepts that follow.

The controversy regarding certain basic concepts.

Were the doubts raised by Gillman, Michelmore and others mentioned above, the only doubts in the field, I should be inclined to present a less thorough, less detailed account of the working concepts of Clements, with whom my own views are in almost complete accord, and should let the dust of controversy raised by other schools alone. But I cannot take this course, for it is perfectly clear from a study of the views of a number of authorities that the time has arrived for a careful review of the highly polemical field concerned with the essential nature and the direction of *succession* and *development*; the nature of the *climax*; the existence of the *complex organism*; and the inherent oneness of the *complex organism* and the *biotic community*.

So far from thinking that an analysis of the various views of others, and the clarifying of points hitherto obscure in my own writings, will have the effect of clearing up all doubts and harmonising the divergent opinions of many workers, I am convinced that if my labours bear any fruit at all, it will be in the direction of stimulating various colleagues to make provocative reply to points I make in this paper.

Objects of the present contribution.

As I feel that, both in the practical sense and in the philosophical, the problems associated with the grand phenomena of *succession*, *development*, the *climax*, the *complex organism*—or to use Tansley's term, the *quasi-organism*—and the community whereof plants and animals are integrated, co-acting constituents, are fundamentally interrelated, I wish to consider these in relation one with another. From analyses of concepts concerning the several subjects I wish to discuss, and from a study of their interrelations, I propose to make certain suggestions which are likely, in my opinion, to be of some utility in practice as well as philosophically.

Where possible and where essential to the illustration of a given theme, I refer to the work of others. While I have access to a reasonable amount of literature, it is more than likely that I have missed points raised in publications unavailable in South Africa. I shall welcome criticism upon this point.

SUCCESSION: ESSENTIAL NATURE AND DIRECTION.

The universality of change.

Whatever precise interpretation we place upon *succession*, we always imply some form or other of *change* in the vegetation of any given area. That change in vegetation with time has been a fact self-evident to every observer has by no means always been true. While Clements (1916, p. 8) tells us that as long ago as 1685 King recorded the process of change in Irish bogs, and traces further contributions on this topic at intervals during the eighteenth century, before bringing us to the studies of Warming (1895), it must be pointed out that *until very recently* the dictum of Cooper (1926, p. 395), that the great majority of Continental ecologists assigned to the dynamics of vegetation a subordinate importance, was true. Although it is clear that a definite alteration in point of view is taking place among the Continental European workers—the book by Braun-Blanquet (1927) on plant sociology being instructive in this respect—it still remains true that a considerable body of workers scarcely shows any appreciation of the importance and the universality of change.

Warming (1895) appears to have been the first to perceive the universality of change, but paid relatively small attention to his important observation, it being left to Cowles (1899, 1901, 1911), Clements (1904, 1905, 1907, 1909, 1916, 1920, etc., to 1934), Moss (1910), Tansley (1920, 1929), and Cooper (1926) to investigate, develop, and apply what Warming incidentally mentions, while it is inherent in the concept of the *biotic community* developed by Clements, Shelford, their associates and Phillips (1931 *a*; *q.v.* for references), that change is universal.

We may accept it as granted that *change* is permanently inherent in vegetation, and therefore may proceed to enquire as to the precise *nature*, the exact *cause* of such change. Is such change due to vegetation itself, i.e. *intrinsic*? Is it due to forces external to the vegetation, i.e. *extrinsic*? Is it due partly to *intrinsic*, partly to *extrinsic* causes? Is the change always *progressive*, i.e. in the direction of a climax or ultimate community, or may it be either *progressive* or *retrogressive* according to circumstances? Innate in these and similar questions are the doubts and difficulties experienced by ecologists, actual and prospective, and indicated in some respects by Michelmore (1934).

Change occurs. Is all change succession? If not, what aspects of change are successional? I attempt to deal with questions such as these in the sections below.

The nature and causes of change.

Concept: Succession is due to any cause, and is either progressive or retrogressive.

According to this concept, succession may be due to any or all of a large number of most diverse kinds of agency, which for brevity can be classified under: *climatic*, *topographic*, *edaphic*, *biotic*, and *biotic reaction* causes. At the same time, it is conceived as a process developing toward a climax, and as one actually capable of proceeding in a reverse direction—from a higher community to a lower. In other words, each and every change in the community, *no matter how occasioned, no matter how proceeding*, is actually included in the process of succession.

With regard to the causes mentioned, I wish to make plain that these, apart from the *biotic reactions*, are to be considered for present purposes of discussion, not in the sense of causes *initiating* succession, but in the sense of their being capable of *continuing* the process; *biotic reactions*, obviously, are continuative. Cowles (1911, p. 168), as is well known, attempted a classification of succession on the basis of *initiating cause*, thus: *regional* (chiefly climatic), *topographic*, and *biotic*. As he did not distinguish between the initiating causes and the continuative cause (namely his *biotic succession* due to the reactions of plants and animals) a considerable amount of confusion arose; this has been increased by reason of Cowles's use of *biotic* agency or factor in a double sense—as an initiating cause, and as the outcome of the reactions of organisms.

To me it seems likely that ecologists who hold the view that succession follows from any cause—be it physico-chemical, a biotic agency, such as a fungus or an insect, responsible for some influence upon the members of the community, or the outcome of reaction of the community upon its habitat—subconsciously must ask themselves to do what I have asked the reader of this section to do: to treat *current* climatic, topographic, edaphic and biotic causes as *continuative* causes of succession. Dealing oftentimes with vegetation that has reached a number of stages from the pioneer, and not being satisfied with the biotic reactions of the community as the sufficient or the only cause for succession, they perforce look elsewhere for causes capable of *continuing* the process. Such causes, they may argue, are resident in the changes in local physiography, in soil water, in an aerial factor-complex such as evaporativity. Having found such considered causes, noting this or that change in the community, they are content that cause and effect have been correlated. From such a basis, dealing with succession from a lower community to a higher, it probably is not difficult to develop the view that climatic, topographic, edaphic, and biotic causes link up with what appears to be a *retrogressive* development: a higher community yielding partly or wholly to a lower. Many will not wish to include in the causes of any such apparent retrogression, any kind or direction of *biotic reaction* such as, they may be prepared to admit, takes place in *progressive* succession. A few—even after going so far as to concede for the sake of argument that the community is a complex organism—will find themselves agreeing with Cooper (1926, p. 403) that there is precedent in the life of the individual organism for the admission of retrogression in vegetation, with the reservation that neither in the individual nor the complex organism is it necessary, in retrogression, to retrace the *exact* steps made during progression.

It is interesting to note the points of view advanced by some ecologists, whose writings, in greater or lesser degree, indicate that they believe in succession following any cause, and going either forward or backward.

Among those who do not appear to have given any *precise* definition of what they have held to be the main causes of succession, but who were emphatic upon the point of the process being retrogressive as well as the reverse, were Nilsson (1899), Graebner (1901), Cajander (1904), Warming (1909, p. 361), Moss (1907, p. 188; 1910, p. 36; 1913, p. 20), Farrow (1918, p. 146). As Clements (1916, p. 146) points out, Nilsson seems to have been the first to distinguish between progressive and retrogressive succession, in his work upon the vegetation around Swedish lakes, and there is little doubt that his treatment formed the basis for the beliefs of Cajander and Moss. Clements (1916, pp. 146–63) presents a full summary of the works and contentions of these workers, and in addition deals with the views of Graebner, so well known for his studies of the processes whereby forest or swamp is converted into heath or heath-moor. The apparent retrogressive stages, in some instances alternating frequently with ordinary progressive stages, seem, both from the accounts of these and other workers, and from Clements's able analysis, to be in all cases accounted for by reason of some disturbing influence, such as flooding, desiccation, grazing, firing, felling, rabbits, this influence destroying an older stage, presenting conditions for an earlier stage, and thus generating an ordinary *secondary* and *progressive* succession.

Among those who state what they consider to be the causes of succession, and at the same time believe in retrogression as well as progression, are Cowles (1901, 1909, 1911, 1919), Crampton (1912), Gleason (1917, 1927), Tansley (1920, 1929), Nichols (1923), and Cooper (1916, 1926, 1926 *a*).

Cowles (1901, p. 82; 1911, pp. 170–1), while basing his classification of successions upon causes—climate, physiography, biota—definitely realised, in those early days, the importance of community reaction. Indeed, he states (1911, p. 171), in discussing the several forms of succession due to climatic change and erosive factors, that it is probably true that the character of the present vegetative covering is due far more to the influence of biotic factors than to the more obvious factors, climatic and physiographic. His belief that succession is retrogressive as well as progressive (1901, p. 81; 1911, p. 170; 1919, p. 478) was based on physiographic grounds: "Retrogressive phases, i.e., away from the mesophytic and toward the hydrophytic or xerophytic, must be included, as well as progressive phases away from the hydrophytic and toward the mesophytic." His concept of retrogression, therefore, is seen to be distinct from that of Nilsson (1899), Cajander (1904), Moss (1907, 1910, 1913) and some more recent authors. It is worth noting, however, that in his 1911 paper (p. 170) he gives the impression of regarding retrogression as much the same as destruction; later (1919, p. 477), he emphasises that while Clements (1916) positively believes that succession is always progressive, he is equally sure that it may be retrogressive, although progression is much more abundant and important. He then adds: "What the reviewer would term retrogressive is for the most part by Clements termed denudation, preparatory to initiation of another successional series." If denudation and retrogression were sudden, he would permit this view to pass, but he urges that in an area *gradually* sinking, there may be gradual retrogression from a climax mesophytic forest to a hydrophytic association with no denudation of any sort whatever.

Crampton (1911, p. 20; 1912, p. 4) apparently considered local initial topographic causes almost universal in influence, and seems to have been ignorant of biotic reaction. The views of Gleason (1917, p. 475) upon causes of succession may be summarised thus: the common cause is an effective change in the environment, which may consist of a change in the physical factors due to inorganic agents, to plant reaction, or to a combination of these; where vegetation is sparse, succession is usually due to changes in the physical environment, but where vegetation is dense, reaction is usually more rapid and effective. As regards retrogression, he states, in reply to the exclusion by Clements (1916), of certain described cases of retrogression, that according to the behaviour of individual plants, the processes are precisely the same as in the usual type of succession. In a more recent paper, Gleason (1927) strongly supports the view that there are retrogressions, decides that the direction of succession is a resultant of forces, and agrees with Cooper (1926) that all sorts of vegetation change are related to succession.

In his analysis of the causes and direction of succession, Tansley (1916, p. 201; 1920, p. 136; 1929, p. 677 et seq.) has done most useful service. He points out that causes are *external* (climatic and physiographic in the grand sense) and *internal*—the latter due to the activities of the plants themselves; he very rightly distinguishes between *autogenic* succession, due to biotic reaction, and that caused by external factors—his *allogenic* succession. Actual succession, he emphasises, commonly shows a mixture of the external and the internal causes. In autogenic or organic succession, he reminds us of the need for separating the communities that are late because they arrive later and develop more slowly, from those communities that depend for their initial establishment and development upon the reactions of earlier stages. With his belief in climatic, physiographic, and organic causes of succession, he is able to support strongly the view that while *development*—or organic or autogenic succession—always is progressive, succession otherwise may be retrogressive. Although he agrees that Clements (1916) largely disposes of the arguments of Cowles and Moss (*op. cit.*) for the use of the term retrogressive succession, as disturbing physiographic and biotic agencies can be shown to be at work in the examples cited by these workers, he is convinced that retrogression does take place. He cites the examples by Farrow (1918, p. 146), and mentions the case of the lowering of ground water-level by increased drainage following increasing erosion, and the further instance of depletion of salts by leaching, both of these appearing to provide conditions for true retrogressive succession. He stresses (1920, p. 137) that such succession has nothing to do with the autogenic process.

Tansley (1929, p. 685) suggests the need for investigation of causes of change, rightly pointing out that these include much more than the habitat factors in the narrower sense, and take into account migration of constituent species, their plasticity, their responses to the habitat, their reaction upon habitat, and details of their interrelations—competition, protection and so forth. In its clear statement and practical as well as philosophical approach, this paper places ecologists in deep debt to its author.

Nichols (1923, p. 168), referring to Tansley's (1920, p. 136) ruling that it is only organically controlled succession in which it is possible to recognise *development*, interprets the concept of development somewhat more liberally. He would regard the changes accompanying the formation of a salt marsh or flood plain, for example, as developmental, despite their not being wholly under organic control, and would describe as *developmental* any succession showing definite progression toward a climax. In a detailed classification of successions, he deals with types of succession in relation to cause, trend, origin, and climax. As regards *cause*, he distinguishes *biotic* succession as being due to influence of plants and animals, *physiographic* succession as due to changes in physiography or physico-chemical nature of the substratum, *climatic* succession due to climatic changes, *anthropeic* succession due to man, and *pyric* succession due to fire. With reference to *trend*, successions may be either progressive or retrogressive; retrogressive succession due to destruction by such agencies as man, erosion, and fire, he terms *cataclysmic*. His *biotic* succession is typically *progressive*—he cites the exceptions such as are illustrated by the effect of fungi and similar destructive agencies, which he considers distinctly *retrogressive* and even *cataclysmic*; this suggests a confusion of biotic reactions with biotic factors, such as was noted in the instance of Cowles (1911, p. 170). While *physiographic* and *climatic* successions, he holds, may be *progressive*, *retrogressive*, or *cataclysmic*, *pyric* and *anthropeic* successions are primarily *retrogressive* and commonly *cataclysmic*, *anthropeic* succession sometimes being *progressive*.

We find that Cooper (1926, p. 401) also takes a very liberal view: succession being the universal process of vegetation change, all vegetation changes must of necessity be succession. All kinds of change—in number and luxuriance of individuals; in species, their number and relative importance—and change due to any cause whatsoever, is succession. He (1926, p. 398) conceives vegetation as a flowing, braided stream of enormous complexity, its constituent currents branched and interwoven, disappearing and reappearing. Present-day vegetation is represented by the advancing front of this stream, in which "we see more or less definite groupings that tend to repeat themselves in space, the advancing termini of the streamlet elements." Strong criticism is directed against the procedure of attributing certain phenomena solely to *internal* and others to *external* causes; organism and habitat form a system, events concerned with one necessarily involve the other. All change is due to the interaction of changing organisms and changing environment. As examples of gradual change in vegetation due to gradual alteration in soil he mentions downcutting by a stream in alluvial soil, the water-table sinking, and slow desiccation of the surface soil resulting; and leaching of soluble salts from soil. Clements, he states, would consider such phenomena "beyond the pale," but his exclusion of such from succession is entirely due to the supposition of identity between unit of vegetation and organism. Discard of this supposition would enable such phenomena to be regarded as truly successional.

Concept: Succession is due to any cause, and is either progressive or retrogressive; but change must be gradual.

This concept is but a slight variation of the foregoing, but nevertheless is worthy of mention by reason of the controversy upon the importance or otherwise of rate of change in the habitat, due principally to erosion, fire, and activities of man directly and indirectly. Tansley (1920, p. 136) considers succession, in its most general sense, as simply the gradual change which occurs in vegetation. Gradual change in climate, or gradual lowering of the ground water-level, produces successions entirely different from those due to organic reactions within a habitat otherwise substantially constant. Cooper (1926, p. 401), referring to Tansley's making *gradualness* the criterion of true succession, is prepared to consider *abrupt* changes in vegetation following abrupt changes in habitat, as succession. This is reminiscent of Nichols (1923, p. 170), who believes in *cataclysmic* succession, in that it concerns the replacement of one plant association by another.

Concept: Succession is due to any cause, and is either progressive or retrogressive; if progressive, due to reactions; if retrogressive, due to causes other than reactions.

Succession may be progressive or retrogressive, and may be due to various causes; if it be progressive, then the *sole* cause is *biotic reaction*; if it be retrogressive, the causes will be *other than biotic reaction*. From what I gather from a careful study of the views of Braun-Blanquet (1932, pp. 310, 325), he is a supporter of this view. He appreciates that there is an ultimate and intimate causal relation between the processes of soil formation and the development of vegetation. Physical factors prepare the way, living organisms then begin to play their parts, and the soil development is directed into definite channels. Since climatic processes proceed according to law, both soil formation and development of vegetation must ultimately be due to the prevailing climate. All seres leading towards the climax are progressive; retrogressive successions—which recede from the climax—are often caused by man or animals, while the spread of moor resulting from a raised water-table is an example of retrogression.

Concept: Succession is due to any cause, but is progressive only.

Succession is produced by physical, biotic and biotic reaction causes, but is always toward a climax, and hence is always progressive. I am not aware that this concept is held by any ecologists who have published, but refer to it as one not unlikely to present itself. Indeed it is a common view expressed by prospective ecologists not conversant with the main theme of development, and with botanists studying applied ecological features in agricultural, forestry, and pastoral problems. A *developmental* succession in the sense of Nichols (1923, p. 169) fits in here, in that Nichols believes it may be produced by causes other than "organic control," and that it progresses toward a climax, no possibility of retrogression being mentioned.

Concept: Succession is due to biotic reactions only, and is always progressive.

Succession takes place in response to the reactions of plant (and animal) constituents of any given community, these reactions being *continuative* causes of succession, as opposed to the climatic, physiographic, edaphic, and biotic *initiating* causes. Succession being developmental in nature, the process must and can be progressive only.

The author and developer of this concept is Clements (1904, p. 124; 1905, p. 257; 1907, p. 282; 1916, p. 80, etc.). While precise details as to their exact views upon cause and direction are not given in most of the works of Clements's co-workers, and in most of the works of the large and growing body of ecologists in the British Empire who have found some or all of his criteria, bases and methods of distinct utility, it is safe to say that an appreciable number of those who have followed Clements accept the basic beliefs: *succession follows on reaction: succession is inherently and inevitably progressive.* In my own experience of twelve years' work in such distinct vegetations as those of the Knysna forest region, the deciduous scrub and savanna region of Tanganyika, and the tree and grass savanna of the highveld of the Transvaal (see Phillips: 1926, p. 366; 1931, pp. 204–9; 1931 *a*, p. 21), I have found very considerable support for these fundamental criteria. These views are brought out simply and clearly in a recent work by Weaver and Clements (1929, pp. 77–9, 145–6), which should be in the hands of all ecologists, prospective and practising. In the course of a correspondence ranging over twelve years, Dr Clements and I have from time to time compared our experiences and the progress of our views, and definitely find ourselves in full agreement upon these criteria and a number of associated points.

It is worth remembering that Tansley (1920, p. 136; 1929, p. 680) accepts *biotic* or *autogenic* succession as *developmental*, and that Nichols admits his *biotic* succession, at least, to be typically *progressive.*

Retrogression and so-called degeneration are considered, on this concept, to be due to some form or other of disturbance, often of the nature of erosion, deposit, changing water-level, leaching, felling, firing, grazing, cultivation. In this connection, I wish to record my view that the use of "retrogression" in a loose sense is likely to cause increasing confusion upon this important and much debated point; for example, Fenton (1934, p. 279) uses *retrogression* where he means *progressive* succession from grass to scrub and woodland.

Michelmore (1934, pp. 313, 315) apparently accepts this concept in part. Such succession he says rarely occurs between the different types of natural vegetation.

This concept receives further consideration in connection with *Development*, and with the *Complex Organism and Biotic Community.*

Concept: Succession is due to any cause except biotic reactions.

Succession is due to climatic and physiographic causes only, biotic reactions being ignored. Perhaps I do Crampton (1911, 1912) less than justice when I include his views under this concept, but it does seem from his works that while he recorded his appreciation of the importance of Cowles's contribution of the *biotic* succession, he failed to separate this from his own topographic successions, which were due to local topographic initial causes. Crampton (1912, p. 4) concludes that the topographic and biotic successions of Cowles show "progressive associations," while "retrogressive associations" are chiefly distinctive of successions which have partly completed stabilisation.

Concept: Succession is due to biotic reactions only, and is progressive and retrogressive.

So far as I know, such a succession has not been conceived. Clements (1916, p. 163), in discussing development, rightly points out that backward development is impossible, as reactions cannot be destroyed *pari passu* with destruction of communities in the reverse order of sequence.

Convergence and divergence.

Convergence of the seres of a climax, naturally, is upon the final community; this is because convergence is an outcome of proper *development.* Convergence is tacitly accepted as a fact by a large number of ecologists studying succession, but actually owes its precise definition to Clements (1916, p. 165). It must be stressed, however, that convergence most frequently is not directly upon the final community, but upon a late medial stage, or a subclimax stage. Diagrammatic examples are seen in some of the charts reproduced by Clements (1916, chapters x and xi). Bews (1920, p. 454), in his study of the ecology of the coast belt of Natal, shows that there is first convergence upon some form or other of coastal scrub, and thereafter upon coastal forest. In my study of the conditions within the Knysna forest region (Phillips, 1931, pp. 107, 124), I suggest convergence of all seres upon "fijnbos" or macchia, while in Tanganyika (Phillips, 1930, pp. 221–2), I suggest for the deciduous scrub succession a convergence in some cases upon *Combretum*-Open Woodland. Michelmore (1934, p. 315), however, considers that the idea of convergence of all the types of a region toward a mesophytic climax is unsound, and has had much to do with another unsound belief: the universal succession of vegetation. Admittedly convergence does occur in some types, but Africa shows that there is differentiation of soils, and consequent *divergence* of those communities that are dependent upon soil types.

Were Michelmore to continue his observations upon divergence, he would probably find what so many have found before him: that apparent, or actual and temporary, divergence within any given sere is followed sooner or later by reconvergence. As Clements (1916, p. 167) has said, and as I have found more than once, *apparent* divergence creeps into our minds and our schematic charts of succession, first, because a particular community—for some reason or another—is able to develop in one portion of a seral area and not in another; secondly, because we erroneously connect *secondary* seres—due to some form of disturbance—with true primary ones; thirdly, because two or more approximately or wholly equivalent communities—in the successional sense—may be found; and fourthly, because there may be an alternation in communities. *True divergence* is not seen within any given climax, but is naturally exhibited when a number of climax regions are considered together. Thus practically identical or closely similar pioneer communities in several climax regions are known to diverge, sooner or later, to form the most dissimilar medial and ultimate communities.

As regards convergence, I am prepared to agree that different geological formations, or different soil types within a geological formation, present greater or lesser variation in the communities they support, a variation reflected to some extent even in the precise portions of the climax communities borne by them. This admission is inherent in my modification of Cajander's (1909, 1926) theory of forest types, as developed for the temperate-subtropical evergreen forests of Knysna (Phillips, 1928, 1931). I imagine that it is resident too, to some extent, in Clements's (1929, p. 198) concept of the *seration*, which its author defines for me in a recent letter as "a kind of local expression of the clisere to be found on the flanks of great mountain ranges. The clisere represents a sequence of climaxes that moves as a unit in the face of climatic changes, as though strung on a string, and the *seration* represents a similar but *edaphic* sequence such as one would meet in crossing a valley from the high lands on either side."

It would probably be well to provide for such edaphic variants in a scheme of classification and nomenclature, on the same lines as those on which Clements (1926, p. 363; 1929, p. 198; 1930, pp. 236–7; 1932, p. 214) subdivides, on a climatic basis, variants in his *associations* into *faciations* (larger subdivisions) and *lociations*, and his *associes* into *facies* and *locies*.

Modifications in succession.

Clements (1904, pp. 107, 122; 1905, pp. 240, 254; 1907, p. 272; 1916, p. 166) has recognised and distinguished various modifications of *normal* succession, while among others, Godwin (in Godwin and Tansley, 1929, pp. 394, 433, and Godwin and Bharucha, 1932, pp. 184, 190) has paid attention to the particular modification known as *deflected* succession. *Deflected* succession is produced when any particular stage or stages are removed, or interfered with, in such activities as grazing, firing, felling, cutting, or draining, the succession progressing *via* stages not normally within the sequence, and ultimately culminating at the normal climax.

Deflected and other *anomalous* successions are especially worthy of recognition and investigation in Africa, by reason of the agelong action of fire in vegetation of many kinds, and the ever-increasing complications introduced by over-stocking, selective grazing, destruction of woody growth by fire and axe, cultivation, and withholding of veld fires. Investigation of succession tendencies in Transvaal highveld grass and tree savanna, during the past two years, leads me to appreciate the possible complications likely to arise from such disturbances—a matter of the greatest scientific and economic importance in the light of the growing attention being given in Africa, Australia, and America to the ecological bases of veld and pasture control.

Increasing information from various scientific fields is likely to clear up many points of difficulty in suspected anomalous succession. An interesting example from Tanganyika is given in Part II, an example due to the critical observations of geologist, geomorphologist and survey botanist (Gillman, 1931, *in manuscript*; Teale, 1931, pp. 12–14).

CONCLUSIONS AND SUGGESTIONS.

On reviewing my own experiences in conjunction with the examination of concepts discussed in this paper, I am able to come to the *conclusions*, and to make the *suggestions*, that follow.

Conclusions.

(1) Succession is the result of *biotic reactions* only. Frequently, however, external factors come into action, and tend to introduce apparent complications—hence I submit *Suggestion No.* 2 in the sequel.

(2) Succession is *progressive* only; all examples of apparent retrogression are explicable in terms of some disturbing agency. In this connection my *Suggestion No.* 2 may be found helpful.

(3) Succession comprises *change in community*, *change in species and in life-forms*, *biotic reactions*, and *development of the habitat* from an extreme to a *medium or normal* condition.

(4) Careful separation of *initiating* causes from *continuing* causes of succession—as has been done so thoroughly by Clements (e.g. 1916, pp. 33, 63)—is essential to a clear understanding of the relative rôle of *external* physico-chemical-biotic factors, and *intrinsic* biotic reactions. Tansley's (1929, p. 680) suggestion regarding the separation of *autogenic* from *allogenic* influences is definitely in support of Clements's (*op. cit.*) clear separation of *biotic initiating* causes from *biotic reactions*—and is thus of distinct interest and value.

(5) It is clear that succession cannot be classified upon *causes*—the difficulties in the way of the suggestions made by Cowles (1911, p. 168) in this connection being apparent both in theory and in practice.

I am in complete accord with Clements (1916, p. 175) in his view that in a *natural* classification *development* must constitute the chief basis.

(6) While careful consideration of details must await special treatment, in Part II, of the concept of the complex-organism, I wish to record at this point my continued feeling that acceptance of the view that the phenomena of succession are inherent in the development of the *complex-organism*, the community, is distinctly enlightening. So far from agreeing with various critics—for example, Cooper (1926, pp. 399–402)—that this view detracts from Clements's great contributions to the investigation of succession, I believe that Clements (1905, p. 199; 1916, p. 3; 1920, p. 52) in this view gave us something definitely fundamental.

(7) *Convergence* toward a climax is the general successional trend of all vegetation I have seen, heard of, or read about. Apparent and true *divergence* must be separated, as indicated under the appropriate heading above.

(8) As opposed to the view put forward by Michelmore (1934, p. 315), I believe that "true intrinsic" succession is the fundamental process linking "the different types of natural vegetation," provided these are within the same climatic region; and in detail are within the same sere within that region. Naturally, within a climax community, successional changes are mere matters of local adjustment—no community in all its parts, and during the whole of its existence, being wholly static.

(9) Michelmore (1934, p. 315) concludes that "the vegetation of a region does not tend toward a single climax type...the real climax or 'natural' vegetation is a whole series of types," determined by climatic, soil and other factors. Since I am dealing with concepts of the climax in Part II, I shall do no more than record here that all my experience leads me to accept the concept of the *monoclimax*—the *climatic climax* of Clements (1916, 1920, etc.). At the same time I desire to draw the attention of ecologists who have inadequate access to literature to the fact that Clements (1926, p. 363; 1929, p. 198; 1930, pp. 236–7; 1932, p. 214) and Shelford (1932, p. 111) have pro-

vided for variations within the climax, in its final and in its seral stages, *on the basis of variations in local climate.* The concepts of the *faciation* and *facies*, the *lociation* and *locies* should be considered carefully by Michelmore and other critics, as well as the concept of the *seration*, providing for edaphic variations.

(10) It seems to be believed by some workers—e.g. Michelmore (1934, p. 313), Gillman (*loc. cit.*)—that communities upon *different soil types*, within a uniform climatic region, cannot be linked successionally. I can but refer such to the galaxy of examples presented in lithoseral, psammoseral, haloseral, hydroseral successions in Africa, wherein, from entirely dissimilar original conditions, *in terms of substratum*, succession produces identical or closely similar medial and ultimate communities. Excellent examples, too, are given by Clements (1916), and Weaver and Clements (1929). (See my Suggestion No. 1 below.)

(11) Clements (1907, pp. 284–6) has given us outlines of certain "*laws*" of succession. To these Bews (1920, pp. 387–8) added an important point: "In a subtropical region, as the succession advances, the vegetation becomes more and more tropical." In a temperate-subtropical region—such as that extending along the coast from the Cape Peninsula to near Humansdorp, Cape Province—I found (Phillips, 1931, p. 204) that as the succession advances, the vegetation becomes more and more subtropical. It would be interesting to have the views of workers in other parts of the world upon this particular point.

(12) Study of modifications of succession is an essential—a point becoming increasingly important now that successional studies are being applied in economic botany of many kinds.

(13) Some years' work in Tanganyika, followed by several years' study in the Transvaal, leads me to emphasise the need for study of succession at extreme and normal points in climatic cycles. Years of minimum, maximum, and intermediate rainfall—with their accompanying temperature and evaporativity relations, grazing and fire hazards—show profoundly different "aspects" within grassland and savanna successions. Clements (1934, p. 41) has recorded the same experience as the outcome of visits, at drought and flood periods, to the grassland of the Niobrara region.

(14) It is perhaps desirable to stress, too, the increasing need for *experimental* study of succession, a phase that has received all too little attention up to the present. Demand in pastoral, agricultural, veterinary, forestry and other economic circles for information upon successional phenomena must hasten the application of experimental methods in the study of this fundamental process.

Suggestions.

With much diffidence I make the suggestions that follow; I make them solely because I feel they may prove helpful to younger and less experienced workers anxious to understand the main principles of the grand process of succession.

(1) In my Conclusions, Nos. 9 and 10, I mentioned the difficulties some workers find regarding variation in community according to *edaphic* type. I feel that it would help such workers were we to admit some descriptive term immediately supplying information upon any important edaphic characteristic. For example, in Tanganyika and elsewhere in Tropical Africa, a seral community showing various *facies* and *locies* according to greater or smaller variations in climate within a general climatic region, is the one termed by me (Phillips, 1930, pp. 210–13) the *Combretum-Other Spp. Open Woodland.* This community is found upon both *eluvial* and *alluvial* soils, as well as upon a variety of *types* of soils within the two main categories. Some interesting details for a limited region are given by Scott (1934). Would it not be helpful were we to distinguish the *Combretum-Other Spp. Associes : eluvial type* from the *Combretum-Other Spp. Associes: alluvial types*?

Or again—I found that the temperate-subtropical evergreen forests of the Knysna region, South Africa, could be divided into distinct *types*, according to such features as geological formation, soil characteristics, soil moisture, ground flora, layer societies, and growth quality and structure of the constituent trees—yet the various *types* were mere variants of the climatic climax associations and consociations, and therefore formation. Undoubtedly edaphic characteristics play a great part in differentiation of the main *types*, which were termed (Phillips, 1928; 1931, pp. 194–9) *dry*, *medium-moist*, and *moist*. Thus we find, for example, a *Podocarpus-Other Spp.* Association, *dry*, *medium-moist*, or *moist type*, the particular type suffix indicating certain edaphic (and perhaps) other characteristics of importance. Personally, I do not think it necessary to coin a special term, but rather incline to leaving the particular descriptive word to the discretion of the worker, this word to be prefixed to the word "type."

(2) If it be concluded that succession takes place only in accord with *biotic reactions*, on the part of the plants and animals making up the communities, and is always *progressive*, it must be realised that physico-chemical-biotic external factors may influence the *rate* and *precise direction* of succession. Thus, a factor-complex or single factor may act in the *same* direction as the *biotic reactions*, and thus *accelerate* succession; may act in the *opposite* direction to the reactions, and thus *retard* succession; may so *modify* the reactions as to cause *deflection* of direction of succession; may act so as to *interrupt* succession; may act so as to *postpone* or even *terminate* the process. Clements (1916, p. 33) has not missed these possibilities, but it is not unlikely that some ecologists have been much worried by the complications that appear to follow in the train of such factors.

I suggest, then, that we admit the use of certain descriptive terms such as *succession-acceleration*, *succession-retardation*, *succession-deflection*, *succession-interruption*, *succession-postponement*, and *succession-termination* to cover the particular local phenomena encountered in this connection.

In this way it would be possible to cover the examples given by Michelmore (1934, pp. 313–14) from the Sudan, the great Tanganyika Plateau of Northern Rhodesia, and the water-logged "lateritic" areas of Central Africa.

(i) The Sudanese example of replacement of Date Palms by Thorn Scrub, following a lessening of the underground water-supply, might be termed—if the normal succession be hydroseral and hence in the direction of decreasing water-content of the soil—*succession-acceleration*. Obviously if the succession be xeroseral—in the direction of an increase in water-content of the soil—the process would be termed *succession-retardation*.

(ii) (*a*) Small plains of badly drained, heavy soil have been formed by certain rivers; these plains are alleged to be similar to the grassy (alluvial) plains ("mbugas," "dambos") I have described as stages in the development of woodland (Phillips, 1930). The grassy plains are separated from *Brachystegia Woodland* by fringes of *Combretaceous Bush*. Since the valleys become more and more filled by deposit of silt from the river and material from the higher country around, Michelmore (1934, p. 314) states that the succession is "undoubtedly towards the grass plain vegetation." Without knowing this region I find it a little difficult to visualise Michelmore's conditions. If he means that *Brachystegia Woodland*—which in East Africa is *always* on eluvial and *never* on alluvial soils—as well as *Combretaceous Bush* is disappearing before open, semi-vlei or swampy, *alluvial* grassland, then I find it easy to describe the phenomena he mentions as *gradual* destruction of higher stages, accompanied by either *succession-interruption* or *succession-termination*. So far as I know it, *alluvial* grassland *never* can develop to *Brachystegia*, but is able to develop to *Combretum-Other Spp. Open Woodland : alluvial type*. By no stretch of the imagination can development of alluvial grassland upon sites formerly carrying eluvial soil and *Brachystegia* be considered either as succession or as succession toward a climax!

(*b*) In the same region, Michelmore reports rivers to be cutting back, and thus draining and leaching the valley floors; accompanying this is invasion of *Combretaceous Bush* upon grassland, *Brachystegia Woodland* ultimately replacing the *Combretaceous Bush*. Here again I must confess to being a little uncertain of Michelmore's full meaning. If he is referring to *eluvial* soils, then the phenomena he mentions possibly find explanation in *succession-acceleration*—drainage aiding the reaction by reducing excessive water-content—a state of affairs not very likely to occur in a succession which I suspect to be *xeroseral* in nature. If he is referring to *alluvial* soils, I can understand the incoming of *Combretaceous Bush: alluvial type* in response to improved drainage, but I can make nothing of the alleged incoming of Brachystegia, which I know only as a community of *eluvial* soils. I am aware of Scott's (1934, p. 225) interesting exception, in the instance of several trees of *B. microphylla* at Kikori, but even these trees I suspect of being rooted actually in eluvial soil.

(3) Michelmore says that in Central Africa the existence of (alluvial) grass plains and other water-logged types is bound up with the presence of laterite pans; I am not sure of what he means by laterite; I rather suspect him to mean pea-ironstone (iron sesquioxide, "ou'klip," murram, pseudo-laterite), which forms impermeable "pans" in areas which have been subjected to leaching of iron from the upper strata of the soil, and redeposit of the iron in concentrated form at varying depths below. (*a*) In some places, he says the lateritic areas are probably drying up, and becoming more wooded. If this be so, I explain it on grounds of a certain amount of drainage acting in the same direction as the biotic reactions—hence an example of *succession-acceleration*. (*b*) In some places, probably, the areas are becoming wetter. This could be explained in terms of increasingly poor drainage following continued redeposit of iron below the soil, the poor drainage acting *against* the biotic reactions, and hence bringing about *succession-retardation*.

I find it fitting to conclude this admittedly inadequate account of succession with the following reminder from one who studied communities other than those made up by plants and animals—communities of man:

"Man may disturb, he may retard or he may aid the natural process of organisation [Clements here suggests 'development'], but the general course of this process is beyond his control."—HERBERT SPENCER.

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REVIEWS

BRITISH AND GERMAN FOREST COMMUNITIES

Anderson, Mark L. *The Natural Woodlands of Britain and Ireland*, with a classification of waste-land communities to assist the choice of tree species. Pp. 32, 7 × 4⅞ inches. Department of Forestry, Oxford. Price 9*d*., postage extra. 1932.

This little pamphlet was written at the request of Prof. Troup for the use of his students. Plant ecologists interested in the British native woodlands will find it very useful to have such a summary, based on first-hand observation, and written by a scientific forester who has had a wide experience of British woodlands and exceptional opportunities of distinguishing woods which owe their origin to fresh plantation from those which are semi-natural (i.e. based on original natural woodland of the same type, though they may be planted up after clear felling), and from the few fragments which are wholly natural.

Dr Anderson distinguishes fifteen types (this word is here used in a general sense and not of course in the sense of the "forest types" of Cajander and many modern foresters), but he makes no attempt to classify them, though he refers incidentally to certain relationships between different types.

It seemed to the reviewer that it might be useful to try to arrange Dr Anderson's types in a system according to what appear to be their true ecological relationships, and this is done in the table on the opposite page. It will be seen that they fit quite well, and with comparatively little rearrangement of sequence, into the scheme given on the right of the table, in which the climax woods are printed in heavy type. The "remarks" printed in the centre of the table are based on Dr Anderson's descriptions and the reviewer's own knowledge, and serve to connect Dr Anderson's categories with the climax types. In two cases (2, Ashwood and 5, Ash-oakwood) the type has been divided into (*a*) and (*b*) in order to distinguish woods which must be distinguished if they are to come into the system. It is clear from internal evidence that Dr Anderson does not know the south and east so well as he knows the north and west, while the reviewer's first-hand knowledge is complementary.

Three climax types of beechwood have to be distinguished owing to the natural dominance of the beech in the south-east on a variety of soils. Dr Anderson describes only one of these. The remaining dominants are sorted out partly by climatic and partly by soil factors. Of only one of Dr Anderson's types (10, Alder-birch community) is the position in the scheme doubtful, and this (like 13 and 14) probably comes into the subalpine and subarctic birchwood group, which extends of course through a considerable range of climatic and edaphic habitats and shows corresponding variety of composition.

Dr Anderson's classification and analysis of "waste land" communities on which tree plantations may be made is interesting and well worth attention by the ecologist, but it cannot be dealt with here. The relatively high fertility (C, i.e. midway in his fertility series) he finds in land (moss or wet moor) dominated by *Eriophorum* communities is noteworthy, and calls for further investigation.

A. G. T.

Dr Anderson's types	*Remarks*	*Beech region and oak-ash region of summer deciduous forest*	*Soil type*
1. Beechwood		**Beechwood**	Shallow calcareous soils
2. Ashwood *a*		Seral ashwood	
2. Ashwood *b*			
3. Ash-alder	Wet climate facies of ashwood	**Ashwood** (outside beech region)	
4. Ash-birch	Transition to subalpine birchwood		
5. Ash-oakwood (*a*)	Transition from limestone ashwood to oakwood on deeper soil		
		Beechwood Seral ash-oakwood	Clays and loams
7. Moist oakwood		**Damp** **Oakwood**	
5. Ash oakwood (*b*)	Oakwood with high proportion of ash owing to wet climate		
6. Alder-willow	Hydro Seral to Damp oakwood: ("Climax" on permanently wet soils)		
8. Dry oakwood		**Dry** **Oakwood**	Sandy loams, sands and gravels, often podsolising
9. Oak-birch	Seral to oakwood or subclimax		
		Beechwood Seral birch-oak: alternatively subspontaneous pine	
		Birch and pine region of Northern coniferous forest	
11. Scots pine		**Pinewood**	Mainly sands and gravels
12. Scots pine-birch	Transition from pinewood to birchwood		
15. Birchwood		**Birchwood** (subalpine and subarctic)	Mainly fine-grained siliceous rocks
10. Alder-birch	? Wet soil or wet climate facies of subalpine birchwood		
13. Birch-rowan	Local (wet climate) facies of subalpine birchwood		
14. Birch-aspen	Local (dry climate) facies of subalpine birchwood		

Schoenichen, Walter. *Deutsche Waldbäume und Waldtypen.* Pp. xii + 208, with 41 maps in the text and 10 photographic plates, 9¾ × 6½ inches. Jena, Gustav Fischer. Price RM 14, bound RM 15.50. 1933.

This book contains a great deal of information about native German trees and forest types which is very welcome to students of European vegetation.

The plan adopted is to give a separate account of each of the dominant trees and of the various forest types which they characterise, the subordinate species, such as apple, pear, service, rowan, cherry and so on, being mentioned only incidentally. The general distribution in Europe and any marked climatic or edaphic preferences are first described, and then the occurrence within the limits of Germany, the kinds of forest which the species forms or of which it is an important constituent, and the associated shrub, herbaceous and moss flora. In the descriptions of forest types quite recent work, much of which has certainly been stimulated by the phytosociological activity of Dr Braun-Blanquet, figures very largely. In this recent work the difficulty of establishing a coherent and satisfactory "system" of the different forest types is very apparent, and also the considerable gaps in knowledge, as the author remarks in his preface. But a careful study of the book certainly gives the foreign student of phytosociology a much fuller, though perhaps not a much clearer, picture of German forest vegetation than he could obtain hitherto.

From the English point of view it is interesting to note that the majority of the forest dominants common to Britain and the continent show the same soil and climatic preferences in both. The "compensation" provided by the damp climate of the British Isles for the edaphic moisture conditioning the occurrence of various species on the continent is evident in several cases.

The dominance of ash on limestone, which, as the late C. E. Moss first showed, is quite characteristic in Britain outside the beech region, seems, however, to have no exact parallel in Germany, though the abundance and vigour of the ash on the dry shallow calcareous soils of the "Muschelkalk" of west Germany is noted. In both countries of course it is common on wet soils with a good supply of nutritive salts, and in both it avoids poor acid soils. The account of the yew is interesting. The author estimates that there are only about 25,000 trees now existing in the whole of Germany. Though yew has been much planted it has suffered severely from over-exploitation. It never forms extensive woods but only small societies, and as in England often accompanies the beech on limestone soils.

The numerous maps showing the distribution in Europe of various trees are useful, but the boundaries are not always very carefully drawn. Thus in several cases a species is marked as reaching the Mediterranean coasts which certainly does not do so. And the boundaries in the British Isles are seldom accurate; but this, as the present reviewer has remarked on other occasions, is largely the fault of British phytogeographers, who have supplied no accurate information on the native distribution of trees in Britain—often a difficult, but seldom a wholly impossible task. A. G. T.

THE AMERICAN PRAIRIE

Weaver, J. E. and **Fitzpatrick, T. J.** *The Prairie.* Ecological Monographs, 4. Pp. 109–295, with 120 figures, 10 × 6⅞ inches. 1934.

This is a general account, full of solid information, of the American Prairie as developed in the states of South Dakota, Minnesota, Nebraska, Iowa, Kansas and Missouri. The authors examined 135 representative areas in this region, varying from 20 to 360 acres in extent. They deal successively with Climate and Soil, Types of Grassland, Distribution of the major grasses within, and Analyses of the several consociations, Relative height growth of the grasses, Minor grasses and grass-like species, Relative importance and distribution of forbs (herbs not of grass-type), Seasonal aspects, Height-growth and physiological activity, Contacts, Invasion and Succession.

The features of the work are the thoroughness and care with which the material is handled, the large amount of accurate quantitative data provided, particularly as regards the structure and distribution of the prairie vegetation, and the large number of excellent photographs (which might however have been somewhat better printed), giving a very clear idea of prairie scenery and structure, and of the habits and growth forms of the more important constituent species.

The rôle of *Poa pratensis* L. (the "Kentucky bluegrass" of the Americans) in prairie will be of interest to European ecologists. This common European meadowgrass is doubtfully a native of North America, but was introduced into the east with the early settlers and spread westwards when the prairie region was occupied in the middle of last century. It is doubtful if it can invade untouched prairie, but has spread far and wide as the result of annual mowing, and especially now that prairie fires have become rare, since burning is very inimical to the species. It succeeds best in the damp lowlands, where it forms, on the average, as much as 9 per cent. of the basal cover, but it also invades uplands, where it averages 4·7 per cent. It owes its success largely to its early growth, being the first to begin in the spring and forming its flower stalks very early in May, before the vegetative growth of the dominant blue-stems (*Andropogon*) has advanced very far. It is particularly vigorous on disturbed soil. Other invaders are few and transient, but local disturbance may let in *Phleum pratense*, *Trifolium pratense*, or *Melilotus alba*. These facts support Cockayne's contention that alien invaders can rarely establish themselves in closed native communities, though when the native vegetation is seriously disturbed, and the competitive powers of its species damaged by human activity, alien species often enter and even become dominant.

Of primary successions the hydrosere and the halosere are described. One would have liked definite evidence that areas which were originally swampy or salt-impregnated really do come to be occupied by climax prairie. Subseres initiated by disturbance—abandoned roads or the soil thrown up by rodents such as the pocket gopher (*Geomys bursarius*)—are of frequent occurrence.

Everyone who has visited the prairies is aware of their charm, the wide horizons of rolling grassland "where the quick cloud shadows trail," and the wealth of vivid colour, continually changing as the various societies of bright flowered plants succeed one another through the growing season. This work will help to recall such impressions and will convey a very adequate picture of this attractive plant formation to those who have never seen it.

The book would have been well worth providing with an index of plant names and page references.

A. G. T.

Wright, C. Harold. *Soil Analysis: a Handbook of Physical and Chemical Methods.* Pp. viii + 236, with 6 figures in the text, 8½ × 5½ inches. Thos. Murby and Co. Price 12*s.* 6*d.* 1934.

With the extensive modern development of soil science a practical guide to the methods of soil analysis has become much needed; and the present work by an author of long practical experience appears to give a very full and careful account of all the ordinary methods in use in pedological laboratories.

A very useful publication would be a small elementary book which would deal only with those features of soils and the methods of measuring them which are of primary importance to the plant ecologist.

A. G. T.

Schröter, C. *Kleiner Führer durch die Pflanzenwelt der Alpen*. Pp. viii + 80, with 24 figures in the text, 7¾ × 5¼ inches. Zürich, Albert Raustein. 1932.

This little book by the veteran Prof. Schröter is a condensed summary of the Alpine plant communities and the conditions of their existence. As a result of the long experience and very wide knowledge of the author it contains an enormous amount of accurate information packed into a small space, and it is to be warmly recommended to an ecologist (or indeed any botanist) visiting the Alps for the first time. It forms an excellent explanatory companion to the same author's well-known *Taschenflora des Alpenwanderers* which contains coloured pictures of all the common Alpine plants. A. G. T.

THE MAY ISSUE OF THE *JOURNAL OF ANIMAL ECOLOGY* (Vol. III, No. 1)

This number contains nine papers, one note, nine reviews, and a hundred short notices of British publications on animal ecology. An innovation is the issue of a duplicate set of these notices (also sold separately from the *Journal*) printed on one side of the paper for use in indexing.

Census studies again form an important part of the original contributions. A census map by S. Cramp and J. H. Ward of swallow and house martin nests in a district near Manchester demonstrates the preference of the former for rural and the latter for urban habitats. W. B. Yapp's map and census of rookeries in West Gloucestershire shows a density of thirty-one breeding rooks to the square mile, and suggests the favourable influence of arable land on rooks. E. Smirnov and W. Polejaeff, in a statistical study of scale-insects on elms in Moscow, prove that over-crowding increases the number of sterile females and so automatically slows down further increase. David Lack extends his theory of subjective habitat selection to cover certain Icelandic birds: it is shown that the habitat is limited rather by the mental make-up of the bird than by limiting factors concerned with food or nesting sites. Moreau reaches a similar conclusion in his important survey of the factors limiting altitudinal distribution in East African birds. This paper also discusses the kind of ecoclimates in which tropical birds actually live. G. D. Hale Carpenter has collected together a number of interesting observations on the natural history of islands on Lake Victoria, with special reference to tsetse flies: the Situtunga antelope (Speke's Tragelaph) and the effects of its grazing on vegetation; and the distribution of butterflies. Both these African papers contain striking photographs of forest scenery. Two papers deal with freshwater animals. H. P. Moon describes comprehensively the littoral fauna of Windermere on different types of shore, and H. D. Slack records the varied winter food of brown trout in the River Test.

A note contains an appeal for information about the distribution of the wood ant in Britain. Reviews deal with the *Journal of Ecology*, African Lakes, a text book on ecology, marine plankton, the spread of the black-necked grebe, the influence of jack rabbits in America on range vegetation, game management, and Scottish islands.

Charles Elton.

NOTE

WOOD ANT ENQUIRY

I AM in search of information in connection with a survey of the distribution of the wood ant, *Formica rufa*, in the British Isles, and the Editor, to whom my thanks are due, has kindly allowed me to insert a questionnaire in this *Journal* in the hope that some of its readers may be able and willing to give assistance. *Formica rufa*, the common wood ant, is also called locally the horse, fallow, or hill ant. It occurs in woods, particularly with coniferous trees, where it builds large mound-like nests of vegetable débris (sticks, leaves, pine-needles, etc.), which may reach a height of 3 ft. or more. These nests are usually made by the side of paths, in clearings and along the edges of wood. The worker is red, with dark brown or blackish brown legs, antennae and abdomen, and the front of the head is also brown. The ant varies in length from a quarter of an inch to nearly half an inch. Answers to the following questions will be appreciated:

(1) Name and situation of wood where species occurs.
(2) Under what trees are the nests built?
(3) Nature of the soil.
(4) How many nests are there in this locality?
(5) Are the ants increasing or decreasing in number?
(6) For how many years have they been there?

I should be particularly interested in records for beechwoods and calcareous soils. Records for localities where this species has now died out would also be of value, more especially if the cause of extinction is known.

Any information, for which I shall be most grateful, should be sent to me direct at the following address: Miss Enid Nelmes, 27 Westbourne Avenue, Acton, London, W. 3.

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